Establishing movement heuristics for voluntary action: Electrophysiological correlates of movement-outcome learning and the sense of agency

Jeffery G. Bednark

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Abstract

Human behaviour is effect-oriented; we perform many different types of movements to obtain and respond to a variety of sensory consequences. In our everyday lives we have the experience of being in control of our movements and the sensory outcomes they elicit. This sense of agency, and the ability to initiate voluntary movements to obtain desired outcomes, originates from learning mechanisms that associate voluntary movements and sensory outcomes that often occur together. It is the anticipation of an outcome that allows for the selection of voluntary behaviour and the experience of control over movements and the outcomes they produce. Thus, movement heuristics that capture the predictive link between movement and outcome are necessary for voluntary behaviour and the sense of agency. Event-related potentials (ERPs) associated with outcome monitoring and evaluation, namely the feedback correct-related positivity (fCRP) and the P3, were examined in this thesis to investigate the cognitive processes mediating the formation of movement heuristics.

To differentiate learning a movement heuristic from previous movement-outcome learning paradigms that establish a simple one-to-one association between movement and outcome, a novel movement-learning task was developed. The task was designed so that multiple movements could elicit the desired sensory outcome, but learning of a movement heuristic depended on principal aspects common across all movements. This task and movement-related control tasks to isolate the learning component were initially tested in healthy controls. The ERP results demonstrated that the formation of a movement heuristic is the result of joint cognitive processes. Performance monitoring processes mediating the fCRP indicated the degree of movement-goal coupling, and the P3 indexed the evaluation of novel sensory information with regard to the preceding movement. It was proposed that the unique roles of the basal ganglia and the anterior cingulate cortex in the plasticity and consolidation, respectively, of movement-related information provided a potential outcome monitoring and evaluation system necessary for learning movement heuristics.

To elucidate whether dysfunction of basal ganglia signalling results in disruption of movement heuristic formation, and potentially altered outcome monitoring, a study was conducted with individuals with mild Parkinson’s disease (PD). In dopamine-medicated individuals with PD there was an overall enhancement in P3 amplitude. Additionally, the
lack of difference in fCRP amplitude suggested an altered outcome monitoring. These results indicated that normal functioning of basal ganglia signalling might be necessary for the proper monitoring and evaluation of sensory outcomes.

Finally, the importance of outcome monitoring and evaluation to the sense of agency, were investigated using a judgment of agency task. Results from this study further emphasised the role of the fCRP as an index of movement-goal coupling, giving rise to the feeling to agency. Furthermore, the subsequent indication by the P3 that the sensory outcome was unanticipated swayed judgment to non-agency. By combining systematic manipulations of tasks along with investigations in a sample of neurologically impaired individuals, the present thesis has used a convergent approach to elucidate functional significance of the fCRP and the P3 in outcome monitoring and evaluation.
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List of Abbreviations

ACC  anterior cingulate cortex
Ag   silver
CC   continuous-cue control task
Cl   chloride
EEG  electroencephalography
EOG  electrooculography
ERP  event-related potential
fCRP feedback correct-related positivity
fERN feedback error-related negativity
fMRI functional magnetic resonance imaging
Hz   hertz
IC   initial-cue control task
kΩ   kilohms
L-Dopa levodopa
msec milliseconds
ML   movement-learning task
PD   Parkinson’s disease
PFC  prefrontal cortex
SR   stimulus-response control task
Chapter 1: General Introduction
Chapter 1
General Introduction

In 1911 Edward Thorndike first postulated the fundamental principle of learning, that the consequences of behaviour shape future behavioural expression. A century on, neuroscience is still establishing the neural underpinnings and cognitive processes that mediate Thorndike’s Law of Effect. Understanding the cognitive processes that underlie the monitoring of behavioural consequences is important because this monitoring process informs future voluntary behaviour. Monitoring of outcomes also gives rise to the sense of agency, or the sense that one is in control over one’s movements and their resultant outcomes. The main goal of this PhD is to investigate these cognitive processes using outcome-related event-related potentials (ERPs).

This chapter first introduces an ideomotor explanation of voluntary behaviour, and proposes the concept of movement heuristics to extend ideomotor theory. Second, the unique roles of the basal ganglia and anterior cingulate cortex (ACC) in the plasticity and consolidation, respectively, of movement-related representations will be described in the context of a potential outcome-monitoring system. Along these lines, how ERPs can be used to elucidate the cognitive processes underlying outcome-monitoring are explained, to demonstrate their relationship to activity of the basal ganglia and the ACC. Third, Parkinson’s disease is reviewed to highlight how dysfunction in basal ganglia signalling can result in disruptions of behavioural expression, and potentially alter outcome monitoring. Finally, the importance of outcome monitoring to the sense of agency, and the sense of agency to outcome monitoring, are discussed.

1.1 Voluntary movements are selected with regard to their anticipated outcome

1.1.1 Ideomotor theory

The ideomotor theory began with the musings of Hermann Lotze (1852). In an eloquent translation of Lotze, William James (1890) declares, “if, in voluntary action properly so-called, the act must be foreseen, it follows that no creature not endowed
with divinatory power can perform an act voluntarily for the first time” (p. 487). On this basis a movement is only considered voluntary if its outcome is foreseen. Thus, voluntary movements are goal-directed and intentional with particular emphasis on outcomes.

The basic tenet of the ideomotor theory is that outcomes control voluntary movements. The representation or image of an outcome governs the selection and execution of the associated movements (Elsner and Hommel, 2001). Movements are represented with respect to their sensory effects, and the voluntary selection of a movement is determined by its anticipated effect on the environment (Greenwald, 1970b). Due to a shared representational domain for movement and perception, movements become defined by their perceived consequences (Prinz, 1997).

The process of discovering contingencies between outcomes and their eliciting movements is called ideomotor learning (Elsner and Hommel, 2001, 2004; Herwig and Waszak, 2009; Waszak and Herwig, 2007). The basic notion is that initially, movements are carried out in an exploratory or incidental fashion, and any changes in the environment are perceived and registered (Elsner and Hommel, 2001; Harless, 1861; Lotze, 1852). Importantly, humans have an innate ability to detect changes in the environment (Sokolov, 1963). In new settings, unexpected sensory effects evoke a rapid involuntary shift of attention known as the orienting response (Luria, 1973; Sokolov, 1963). The orienting response is thought to function as a ‘what-is-it’ detector, permitting the unexpected sensory effect to enter awareness (Friedman et al., 2001). Thus, the orienting response facilitates the formation of a new neural representation for the unexpected sensory effect (Sokolov, 1969), making it essential in ideomotor learning.

Initially, Elsner and Hommel (2001) investigated ideomotor learning by instructing participants to freely perform a left or right finger key press. In the acquisition phase each key press was associated with either a high or low tone. In the subsequent test phase, key press responses to tones that were compatible with the acquisition phase had lower reaction times than stimulus-response mappings that were incompatible with the acquisition phase. Subsequently, Elsner and Hommel (2004) demonstrated that only movements and effects that consistently occur together with tight temporal contiguity are associated together. Along these lines, it is proposed that
the consistent temporal overlap between the motor pattern of a movement and the sensory pattern of the perceived sensory outcome results in the automatic association between movements and sensory outcomes (Elsner and Hommel, 2001, 2004; Hommel et al., 2003).

It is important to note that this ideomotor learning process is unique to intentional-based movements (Herwig et al., 2007; Herwig and Waszak, 2009). In fact, the intentional performance of a movement alters the perception of time between the movement and a sensory outcome, so that they appear closer in time (Haggard et al., 2002). Additionally, the ideomotor theory is differentiated from other learning approaches in that it emphasises the acquisition of voluntary actions without the outcome of an action having affective (directly rewarding) consequences (Hommel, personal communication). Indeed, the affective role of outcomes is a key tenet to many dopamine-mediated learning theories. However, recent evidence has shown that the acquisition of new voluntary actions and the elicitation of dopamine signals can occur with non-affective stimuli (for a review see Redgrave & Gurney, 2006). Thus, the emphasis on non-affective stimuli lends strength to the ideomotor approach.

1.1.2 Movement heuristics

The ideomotor theory provides a simple but constructive framework for understanding voluntary movement with the basic tenet that outcomes govern voluntary movements (Elsner and Hommel, 2001). However, learning would lack the required flexibility necessary for acquisition of adaptive behaviours if only a one-to-one association was established between intentional movements and outcomes (as formed in most ideomotor learning paradigms). Take for example opening a door: different doors have different door handles, located at different heights, opening in different directions, etc. If learning how to open a door established only a one-to-one association, then each time we encountered a new door a whole new learning process would have to occur and our minds would have to contain an endless catalogue of movement-outcome associations. Indeed, as highlighted by Franz & McCommick (2010), there is a tendency in the brain to economise cognitive resources, while at the same time optimising behaviour. Further, the brain is continually monitoring sensory and cognitive information to glean essential associations used to efficiently guide behaviour (Bar, 2007).
The concept of a movement heuristic, or an efficient set of rules to guide future movements, is proposed in the present thesis. As a result, learning would require the principal aspects of the movement(s) eliciting a sensory effect to be gleaned. This may include the specific mechanics of a movement, but also the end location of a movement, how or when a movement is performed, the sequence of movements, or any other parameters or combination of parameters that are consistently co-occurring with the effect. Indeed, the ideomotor theory highlights a crucial point of the learning; the outcomes of movement are paramount. Thus, a system of outcome-monitoring would be required to: 1) register the outcomes of intentional movements, 2) evaluate if the outcome has behavioural ramifications, and 3) integrate relevant information in the movement heuristic to guide behavioural selection. In the following section, how an interaction between the basal ganglia and the ACC may provide the neural underpinnings of this outcome-monitoring system is reviewed (Figure 1.1).

Figure 1.1 The proposed outcome-monitoring system. A looped architecture allows for an interaction between anterior cingulate cortex (ACC) and the basal ganglia (modulated by dopamine activity) to register, evaluate, and integrate sensory and motor information into a movement heuristic.

1.2 An outcome-monitoring system

1.2.1 The basal ganglia: Registering outcomes and converging on the causal aspects of movement and context

The role of the basal ganglia in outcome-monitoring stems from its proposed selection architecture (Prescott et al., 2006; Redgrave et al., 1999), and the involvement
of striatal dopamine in the discovery of novel actions (Redgrave and Gurney, 2006; Redgrave et al., 2008). Indeed, since the late nineteenth century the basal ganglia have been synonymous with adaptive behaviour (Ferrier, 1876). As will be described below, the abundant efferent and afferent projections, modulatory activity of dopamine, and functionally segregated corticostriatal loops make the basal ganglia well suited for adaptive behaviour.

The basal ganglia comprise a collection of interconnected subcortical nuclei, with extensive connections to cortical and subcortical structures via a parallel looped architecture (Alexander et al., 1986; McHaffie et al., 2005). The striatum serves as the primary input nucleus of the basal ganglia, receiving afferent projections from external structures as well as modulatory input from other basal ganglia nuclei (Di Chiara et al., 1994). In primates, the striatum consists of the caudate nucleus and the putamen. The primary output structures are the internal globus pallidus (GPi) and the substantia nigra pars reticulata (SNr), which convey tonic inhibitory signals to target structures in the thalamus (projecting up to the cortex) and brainstem. Dopamine activity shapes basal ganglia output by modulating synaptic activity within the intrinsic structures of the basal ganglia, primarily within the striatum (Bjorklund and Dunnett, 2007).

Dopamine activity helps to configure basal ganglia intrinsic structures to mediate movement selection (Redgrave and Gurney, 2006; Redgrave et al., 2008). During movement selection the input nuclei of the basal ganglia receive input signals from external structures, and through an intrinsic process of comparing the ‘salience’ of the different input signals (adjusted by dopamine activity), they select which input structure should be given control over motor resources (Redgrave et al., 2008). The reinforcement learning mechanism mediated by the dopamine signal that helps to configure this selection process also has a critical role in monitoring behaviourally salient sensory events (Redgrave et al., 2008).

There are two patterns of dopamine cell firing activity, resulting in two different types of dopamine signals: phasic and tonic (Grace, 1991). While the tonic signal is proposed to mediate movement selection processes in the basal ganglia (Mink, 1996; Redgrave et al., 1999), the phasic signal is particularly important for detecting relevant sensory outcomes and converging on the causal aspects of movement and context (Redgrave and Gurney, 2006; Redgrave et al., 2008). Phasic activity is typically
induced by unexpected rewards/sensory events (Schultz, 1998) or behaviourally relevant stimuli (Zink et al., 2003). This elicits burst firing of dopamine neurons, leading to a phasic increase of dopamine levels within the striatum (Freeman et al., 1985; Horvitz et al., 1997; Schultz, 1998). Thus, the time-specific phasic dopamine signal indicates the occurrence of a behaviourally relevant sensory event (Redgrave and Gurney, 2006; Redgrave et al., 2008; Zink et al., 2003). Through modulation of the efficacy of corticostriatal synapses (Reynolds et al., 2001), the phasic dopamine signal also strengthens recently active motor and context inputs to the striatum (Figure 1.2). By identifying the outcomes for which our movements are responsible, the time-specific and reinforcing phasic signal has a role in the sense of agency (Redgrave and Gurney, 2006). Finally, through selective disinhibition of basal ganglia output structures, this information is conveyed to cortical structures for further evaluation (Kimura and Graybiel, 1995).

Figure 1.2 Convergent input into the basal ganglia as a potential indicator of agency. Adapted from Redgrave, Gurney, and Reynolds (2008). The figure highlights the four afferent signals in the striatum: (i) Efferent motor copy of recently performed movements (green arrows), (ii) cortical signals provide task/environmental contextual information (blue arrow), (iii) sensory information (green stimulus) is conveyed by the superior colliculus via the thalamus (red arrows), and (iv) activation of dopamine signalling (orange arrow) by unexpected sensory outcomes would strengthen recently active motor (green arrow) and context (blue arrow).
The stage of learning (which is related to the unexpectedness of the sensory event) and the mode of the preceding movement (intentional or habitual) dictate the basal ganglia and cortical regions to which this movement-related information is conveyed. Cortical projections to the striatum are segregated based on the function of the region contributing the cortical afferents (Parent, 1990; Parent and Hazrati, 1995). As such, cortical regions associated with sensorimotor, associative, and limbic functions are projected in a partially segregated manner onto different striatal territories (Parent, 1990). Sensorimotor regions project to dorsolateral striatal territories, associative regions project to the area between the ventromedial and dorsolateral striatal territories, and limbic regions project to ventromedial striatal territories (Redgrave et al., 2010). This organization is generally maintained through the basal ganglia and projections from this complex back to the cortex via the thalamus, forming partially segregated cortico-striatal loops (Parent and Hazrati, 1995).

Functionally segregated cortico-striatal loops have been proposed to mediate different modes of adaptive behaviour (Balleine and O'Doherty, 2009; Redgrave et al., 2010; Yin and Knowlton, 2006). Based on functional models, goal-directed control is mediated by the associative loop, habitual control is mediated by the sensorimotor loop, and motivational input is provided by the limbic loop (Balleine and O'Doherty, 2009; Redgrave et al., 2010; Yin and Knowlton, 2006). Additionally, the associative loop and the sensorimotor loop are proposed to be differentially involved in the early and later stages of learning, respectively (Ashby et al., 2010). With regards to the outcome-monitoring and the formation of a movement heuristic, the associative loop is particularly important since it mediates goal-directed movements and is critical for the early stages of learning. Importantly, the associative loop has connections to the prefrontal cortex, including portions of the ACC (Balleine and O'Doherty, 2009; Redgrave et al., 2010), allowing for the evaluation of movement and outcome information.

1.2.2 The anterior cingulate cortex: Evaluating and integrating outcome-related information to guide future behaviour

The ACC is vital to outcome monitoring (Rushworth et al., 2007a; Walton et al., 2004) and is responsible for the generation of outcome-related event-related potentials (Zhou et al., 2010). Indeed, the distinct role of translating intentions into
actions has been attributed to the ACC (Paus, 2001). The ACC directly influences movement selection through its dense projections to the motor cortex and spinal cord (Dum and Strick, 1991; Morecraft and van Hoesen, 1992), and potentially in an indirect fashion through projections to the ventromedial and dorsolateral striatal territories (Ferry et al., 2000). With extensive reciprocal connections to the prefrontal cortex (PFC) and afferent projections from the thalamus, the ACC can integrate cognitive and affective information to guide movement selection (Paus, 2001). In addition, through modulation of norepinephrine (Aston-Jones and Cohen, 2005) and dopamine release (Garzano and Groves, 1988) the ACC can alter the likelihood that a movement is selected, and subsequently monitor the outcomes of the movement. In turn, norepinephrine and dopamine can modulate ACC activity (Paus, 2001). Imaging studies have shown that ACC activity is enhanced by administration of the dopamine agonist, apomorphine (Grasby et al., 1993; Kapur et al., 1994).

Given its unique connections and neurophysiology, the ACC is thought to guide voluntary movement selections based on the reinforcement history (i.e. collection of previous outcomes) of previous movements (Holroyd and Coles, 2008; Rushworth et al., 2007a). This is carried out by the ACC assigning values to movements based on their associated reinforcement histories (Rushworth et al., 2007a). This notion is similar to the main proposition of the ideomotor theory, that movements are selected based on their anticipated outcomes. In a previous study, Kennerley et al. (2006) found that monkeys with lesions to the ACC selected actions based on the most recent outcome, rather than a reinforcement history. This finding reinforces the notion that dopaminergic action has a slower time course in the ACC than in the basal ganglia (Lapish et al., 2007). Pasupathy and Miller (2005) have demonstrated that learning-related changes in neural activity occur faster in the basal ganglia, while these changes in the PFC occur more slowly but concurrently with improvement in performance. Thus, the slow dopamine activity in the ACC may mediate the formation of reinforcement histories.

Dopamine may modulate the updating of reinforcement histories via differential effects on its D1 and D2 receptors (Lapish et al., 2007; Seamans and Yang, 2004; Tranatham-Davidson et al., 2004). Dopamine has long-lasting bimodal effects on cortical neurons. This allows for: 1) decreased distractibility to maintain representations
of previous inputs by activation of D1-dopamine receptors (Compte et al., 2000; Durstewitz and Seamans, 2002; Durstewitz et al., 2000a; Durstewitz et al., 2000b), and 2) increased flexibility for evaluating new inputs through activation of D2-dopamine receptors (Durstewitz et al., 2000a; Durstewitz et al., 2000b). This bimodal effect of dopamine in the ACC would allow for the updating and maintenance of the value of a movement over a series of multiple outcomes, rather than only on a single outcome basis. Support for this comes from previous studies that have shown that neurons in the ACC encode reinforcement probabilities (Amiez et al., 2006).

The ACC has a prominent role in the goal-directed control of voluntary movements, particularly during the initial learning of these movements. A study by Walton et al. (2004), found that activity in the ACC was highest when movements were freely chosen and participants had to monitor the outcome of their movements. This activity was high for both correct and incorrect feedback. However, activity in the ACC was minimal when the experimenter chose movements and the outcome did not inform behaviour. It was concluded by Rushworth et al. (2007a) that, “the ACC might not simply be the route by which reward history influences voluntary action choice but it might be the route by which action values are initially explored and established” (p. 171). This is in contrast to proposals that the key function of the ACC is conflict monitoring (e.g. Botvinick et al., 1999; Botvinick, 2007; Botvinick et al., 2004; Kerns et al., 2004) and error detection (e.g. Brown and Braver, 2005; Carter et al., 1998; Debener et al., 2005; Swick, 2002; Yeung et al., 2004). As pointed out by Rushworth et al. (2007c), lesioning of the ACC does not impair performance on conflict monitoring tasks. Additionally, while there is much evidence demonstrating that the ACC is active during the detection of errors, there is also evidence for ACC activity following positive feedback (Matsumoto et al., 2003). As such, ACC activity appears to be dependent on the outcome’s value for informing task performance, rather than on the valence of the outcome (Behrens et al., 2007; Rushworth et al., 2007c).

In summary, the ACC has the unique responsibility of generating exploratory voluntary movements, and monitoring their outcomes to create reinforcement histories that can guide movement selection. As such, ACC activity coupled with output from the basal ganglia (mediated by dopamine) provide an outcome-monitoring system that is essential for ideomotor learning. Through phasic dopamine signalling, the basal
ganglia identify novel and/or behaviourally significant outcomes. These outcomes can then be evaluated and integrated into a reinforcement/outcome history in the ACC to guide future movements. The outcome-related event-related potentials dependent on ACC (and other prefrontal cortical regions that project to the ACC) and basal ganglia activity are reviewed in the next section.

1.3 Event-related potentials of outcome monitoring and evaluation

Various studies have used electroencephalography (EEG), in particular event-related potentials (ERPs), to examine the cognitive processes underlying outcome monitoring and learning. EEG techniques have advantages over other imaging techniques (fMRI/PET) in that they offer better temporal resolution (milliseconds vs. seconds) and a more direct measure of the activity of neurons. While the use of EEG to identify activity within specific brain regions is limited, EEG studies with neurologically-impaired individuals, neuropharmacological manipulations, coregistration of fMRI activity, source-localisation techniques or tasks known to activate specific brain structures can overcome this limitation. Once established, an EEG measure can be used to elucidate the underlying cognitive processes of various human behaviours and responses. Given that most of the EEG studies investigating outcome monitoring and learning have used ERPs, it is useful to briefly describe the ERP technique before discussing outcome-related ERPs, the P3 and the fCRP.

1.3.1 What are ERPs?

An ERP is a “scalp-recorded neural activity that is generated in a given neuroanatomical module when a specific computational operation is performed” (Luck, 2005, p. 59). ERPs are used to measure the occurrence and extent to which the brain is performing different computational operations. The ERP waveform, containing different ERP components (Figure 1.3), is derived from the coarse electroencephalogram (EEG) using signal-averaging techniques. By averaging EEG recordings that are time-locked to the occurrence of multiple sensory, cognitive, or motor events, the ERP technique attempts to isolate specific cognitive processes (Luck, 2005). ERPs are commonly measured with regard to their amplitude (i.e. voltage change from baseline) and latency (i.e. time from event onset). Early ERP research focused on understanding the cognitive processes that gave rise to the different
components of the ERP waveform. One of the first ERP components to be studied was the P3.

One important issue to address when conducting ERP experiments is component identification. As highlighted by Luck (2005), different ERPs often overlap in the waveform. As a result, it is important first to understand the psychological underpinnings of component(s) under investigation. This includes the type of eliciting stimuli, and the psychological context in which the component is elicited. Furthermore, the distribution of the component on the scalp can also help distinguish overlapping components. Scalp distribution is the location on the scalp where an ERP component reaches maximal amplitude. If component(s) have different neural generators their scalp distributions should also demonstrate a degree of difference. Another method for separating overlapped components is the use of difference waves. A difference wave is computed by subtracting an ERP waveform from another ERP waveform that is elicited by different stimuli or in a different psychological context. By subtractive logic, the ERP components mediating any difference between the two waveforms are highlighted. In this thesis, all of these component identification procedures are employed to isolate the two components of interest: the novelty P3 and the fCRP.

Figure 1.3 An example ERP waveform showing the common ERP components. Components with a positive deflection are denoted with a P, while components with a negative deflection
are denoted with an N. The numbers following indicate the position of the component within the waveform. Free Software Foundation ©

1.3.2 The P3 is an index of outcome evaluation and a predictive indicator of learning

The discovery of the P3 by Sutton, Braren, Zubin, and John (1965) launched the ERP research field. From the time of its discovery, the P3 has become the most studied ERP, resulting in numerous reviews outlining its influences, neural origins, and functional significance (e.g. Friedman et al., 2001; Johnson, 1988; Linden, 2005; Polich, 2007; Polich and Comerchero, 2003).

The P3 is defined as the positive deflection in the ERP waveform that peaks 300ms from a time-locked event. The preeminent theoretical account of the P3 is based on the context-update theory (Donchin and Coles, 1988), in which the P3 measures cognitive processes associated with the updating of working memory (Polich, 2007). Stimulus probability (Duncan-Johnson and Donchin, 1977; Squires et al., 1976) and inter-stimulus or target-to-target intervals (Gonsalvez and Polich, 2002) are the conventional stimulus parameters affecting the amplitude of the P3. Work by Squires, Squires, and Hillyard (1975) established that the P3 could be divided into subcomponents: the frontally maximal P3a and the parietally maximal P3b. Accordingly, these P3 subcomponents have been associated with different cognitive processes. While the P3b is largely associated with working memory updating, the P3a is linked to the brain’s orientation response (Friedman et al., 2001). Attentional resource allocation underlies both subcomponents (Kok, 2001).

The involvement of the P3 in updating, orienting, and attention allocating suggests that it reflects cognitive processes necessary for evaluating outcomes. Indeed, previous studies have demonstrated that the P3 is implicated in cognitive processes for the evaluation of both positive (e.g. Hajcak et al., 2005; Wu and Zhou, 2009; Zhou et al., 2010) and negative outcomes (e.g. Falkenstein et al., 1999; Nieuwenhuis et al., 2001; Overbeek et al., 2005; Ridderinkhof et al., 2009). The presence of a P3 following both positive and negative outcomes has been suggested to reflect the motivational significance of the outcome (Ridderinkhof et al., 2009).
The P3 appears to be particularly sensitive to the evaluation of outcomes that follow action. Zhou, Yu, and Zhou (2010) found that outcomes following action modulate P3 amplitude to a greater degree than outcomes following inaction. Along these lines, it has been suggested that the P3 reflects the updating of an internal model of the movement environment (Krigolson et al., 2008). As a result, the P3 may index the proposed ACC process of updating the reinforcement history of a movement. Indeed, source localization techniques have identified the ACC as the source generator for the P3 associated with actions-outcome evaluation (Zhou et al., 2010).

The most striking feature of the P3 with regard to the formation of movement heuristics is that its amplitude demonstrates learning-related changes (e.g. Bellebaum and Daum, 2008; Groen et al., 2007; Jongsma et al., 2006; Sailer et al., 2010). Sailer et al. (2010) found that P3 amplitude reduced across learning phases in high-learners, but not in low-learners. Additionally, P3 amplitude was predictive of the percentage of correct responses, and it was concluded that the P3 is directly related to task performance. This finding dovetails with Pasupathy and Miller’s (2005) finding, described previously, that learning-related changes in PFC neural activity occur concurrently with improvement in performance. While learning reduces P3 amplitude, the extent to which the P3 demonstrates learning-related changes is modulated by the probability of an outcome. If the probability that a stimulus will occur is still low following learning, P3 amplitude will be maintained because the stimulus maintains a level of unexpectedness despite learning (Bellebaum and Daum, 2008). Building upon the idea that rapid learning-related changes in the basal ganglia may provide an updating signal to the cortex (Pasupathy and Miller, 2005), it has been found that the unique information conveyed by a surprising stimulus determines the trial-by-trial fluctuations in P3 amplitude (Mars et al., 2008).

The novelty P3, which is a specific frontal aspect of the ubiquitous P3, may be a specific index of movement-related outcome evaluation. Various studies have demonstrated that an unanticipated outcome of a voluntary response elicits a novelty P3 with an enhanced amplitude compared to the novelty P3 elicited by an anticipated outcome of a voluntary response (Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007). Therefore, the novelty P3 is associated with evaluation of novel unexpected effects (Friedman et al., 2001). Importantly, the amplitude of the novelty P3
demonstrates plasticity in that it reduces in amplitude with repeated presentations of an initially novel stimulus (Courchesne et al., 1975; Friedman and Simpson, 1994; Kazmerski and Friedman, 1995). The habituation of the novelty P3 is proposed to indicate that its underlying neural mechanisms facilitate the formation of a new neural representation so that a “novel” stimulus is no longer unexpected (Friedman et al., 2001). Specifically, Barcelo et al. (2006) found that both novel tones and cues for task switching elicited a novelty P3. As a result, it was concluded that the novelty P3 reflects cognitive processes necessary for updating task-set information that guides goal-directed movement selection.

In summary, the enhancement of the novelty P3 to unanticipated outcomes of voluntary movements, and the presence of the novelty P3 following cues for task-switching, highlight its potential role in updating movement heuristics. Additionally, the observed learning-related reduction in P3 amplitude and presence of the P3 in response to both positive and negative outcomes points to the fact that this updating signal is specific to improving behavioural performance. Once behaviour is optimized and the occurrence of the outcome is predictable, there is no longer a need to update the movement heuristic and a P3 would not be elicited. However, before outcomes can be evaluated, they must first be registered. Additionally, if the outcome of a selected movement were still valuable or significant after learning, it would be important to monitor whether the desired outcome was achieved. As reviewed below, the fCRP may be a potential index of this registration and monitoring process.
1.3.3 The feedback Correct-Related Positivity (fCRP) is an index the significance of an outcome

The feedback correct-related positivity (fCRP) is a positive-going deflection in the time range of the feedback error-related negativity (fERN, also: feedback related negativity) following positive feedback (Holroyd et al., 2008). Prior to the proposal of Holroyd, Pakzad-Vaezi, and Krigolson (2008), the positive-going deflection within 200-300ms (Figure 1.4) was referred to as the P2a (for anterior P2), P3f, frontal polar component, or frontal selection positivity and was enhanced by task-relevant stimuli (Kenemans et al., 1993; Makeig et al., 1999; Potts et al., 1996; Potts and Tucker, 2001) and more recently the component has been referred to as the reward positivity (Foti et al., 2011; Holroyd et al., 2011). As suggested by Potts (2004) these components are likely the same component, and for consistency will be referred to as the fCRP. The emphasis of task-relevance to the fCRP was highlighted by the finding that in a visual oddball task, the fCRP was only enhanced to target (task-relevant) stimuli but not to infrequent irrelevant stimuli (Potts et al., 1996). Additionally, fCRP amplitude is further enhanced by stimuli that are behaviourally relevant. For example Potts (2004) found that the fCRP to task-relevant stimuli requiring an overt response was enhanced compared to the fCRP to task-relevant stimuli that were passively monitored. With
regards to monitoring the outcomes, it was suggested that because the fCRP is responsible for the modulation of fERN amplitude, the fCRP would indicate the achievement of a task goal (Hajcak et al., 2006; Holroyd et al., 2008).

It has been suggested that the fCRP is the influential component of the fERN (Holroyd et al., 2008), and there is strong evidence supporting the role of the ACC in the generation of the fERN (Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Miltner et al., 1997; Müller et al., 2005; Zhou et al., 2010). Thus, the fCRP is likely related to the outcome-monitoring process of the ACC. In fact, Holroyd, Pakzad-Vaezi, and Krigolson (2008) proposed that the fCRP reflects phasic increases in dopamine neuron activity carried by the midbrain dopamine system to the ACC. Supporting the link between dopamine activity, the ACC and the fCRP, studies have demonstrated that unexpected rewards elicit an fCRP (Potts et al., 2006), and that amphetamine (an indirect dopamine agonist) enhances the amplitude of the fCRP/P2a following presentation of a behaviourally-relevant stimulus (de Bruijn et al., 2005). Thus, the fCRP may reflect basal ganglia signalling to the ACC and identify the outcomes for which our movements are responsible. Additionally, with regards to the sense of agency, very recent studies have demonstrated that the ability to make a choice and the perceived control over outcomes were associated with modulations of the fERN (Li et al., 2011; Peterson et al., 2010).

Overall, the fCRP and the P3 are useful for investigating the cognitive processes necessary for the formation of movement heuristics. The fCRP appears to reflect outcome registration and identification processes in the basal ganglia that are relayed to the ACC. On the other hand, the P3 (specifically the novelty P3) reflects the engagement of evaluative processes to update the movement heuristic, if the sensory outcome is unanticipated by the current heuristic. In order to investigate the potential roles of the fCRP and P3 in this monitoring and learning process, it is important to conduct tasks (these are later described in the first experimental chapter) to dissociate the contribution of the fCRP and the P3. In addition, conducting studies in participants with neurological disorders involving dysfunction of the basal ganglia and/or the ACC is also crucial to examine the cognitive processes that underlie the monitoring of behavioural consequences. In this thesis, these outcome-related ERPs were recorded in individuals with Parkinson’s disease (PD) to gain a better understanding of outcome
monitoring, and to contribute to a neuroscientific understanding of PD. The next section reviews how the disease and commonly prescribed medications may alter movement representation and outcome monitoring.

1.4 The fCRP and novelty P3: Dopamine mediated learning and salience detection

Now that a brief introduction into the general theories and potential uses of the fCRP and the novelty P3 for investigating learning has been presented, it is important to further discuss the specific theories relating the two components to dopamine activity.

1.4.1 The reward prediction error (RPE) theory of the fCRP

Before delving into the reward prediction error (RPE) theory of the fCRP (and the related fERN), a working definition of the fCRP is helpful to evaluate this theory. Holroyd and colleagues have defined the fCRP as a component that “is elicited by a neural system that evaluates in a context-sensitive manner whether or not a task goal has been achieved” (Holroyd et al., 2011, p. 249). However, in the same article Holroyd and colleagues offer a second definition of the fCRP based on the RPE theory. For this working definition the fCRP “is elicited by reward-related events that deviate from expectation” (Holroyd et al., 2011, p. 249). At first glance these two definitions appear somewhat inconsistent. In one instance the fCRP is dependent on monitoring tasks goals, while in the second instance it is dependent on reward expectation. However, these two definitions may not be mutually exclusive; the fCRP could be generated by a neural system that is both sensitive to goal monitoring and reward expectation.

The RPE theory of the fCRP stems from the reinforcement learning theory of the error-related negativity (RL-ERN theory) proposed by Holroyd and Coles (2002). RL-ERN theory posits that the fERN following negative or error feedback is the result of the phasic pause in the dopamine signal carried by the midbrain dopamine system to the ACC (Holroyd and Coles, 2002). This proposal is related to three key observations about the dopamine system and source localisation EEG studies. First, phasic firing of dopamine neurons is induced by the presentation of an unexpected reward (e.g. Ljungberg et al., 1992b; Schultz et al., 1997), but there is a phasic pause in dopamine neuron firing when a predicted reward is not presented (e.g. Hollerman and Schultz,
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1998) or when a punishing stimulus is presented (Coizet et al., 2006). Additionally, the phasic response diminishes as the reward is predicted (Ljungberg et al., 1992b; Schultz et al., 1993). Second, the ACC is innervated by the mesocortical dopamine system (e.g. Gariano and Groves, 1988; Gaspar et al., 1989). Third, dopamine appears to have an inhibitory effect on ACC activity (Bunney and Aghajanian, 1976; Reader et al., 1979). Finally, various EEG source localization studies have linked generation of the ERN and fERN to the ACC (e.g. Miltner et al., 1997; Zhou et al., 2010).

Accumulating evidence that a majority of the modulation observed in fERN amplitude is due to activity in response to correct or positive feedback (Eppinger et al., 2008; Hewig et al., 2008; Holroyd and Coles, 2008; Potts et al., 2006) and the suggestion that the fERN is really an N200 (Holroyd, 2004; Holroyd et al., 2008) is inconsistent with the emphasis on the phasic pause in RL-ERN theory. This is highlighted by the fact that the N200 is generated by a variety of stimuli that are not directly related to error or negative feedback (for a review see Folstein and Van Petten, 2008). To maintain the RL-ERN theory, a recent adaption (RPE theory) has placed more emphasis on the phasic dopamine in response to unexpected correct or rewarding feedback (Holroyd et al., 2008). Thus, a key question is whether the fCRP is elicited under conditions that are known to induce the phasic dopamine firing.

In a straightforward experiment using an experimental paradigm known to induce phasic firing of dopamine neurons, Holroyd et al. (2011) found that the fCRP was present and enhanced under these conditions. However, in the same study Holroyd et al. (2011) found that a smaller fCRP was also elicited by a fully predicted reward stimulus. Yet others have shown that fully predicted reward stimuli no longer elicit a phasic dopamine response (Ljungberg et al., 1992b; Schultz et al., 1993). Thus, while the amplitude of the fCRP is enhanced under conditions known to elicit phasic dopamine responding, it is unlikely that phasic dopamine signalling to the ACC is the sole neural generator responsible for the producing the fCRP. In fact, an EEG study using advanced source localisation has identified the basal ganglia as the likely origin of the fCRP response (Foti et al., 2011).

1.4.2 Basal ganglia origin of the fCRP

A basal ganglia generator of the fCRP would allow for enhancement of the fCRP by phasic dopamine, while still allowing for modulation of the fCRP by the
achievement of task goals. The nuclei of the basal ganglia are both the generators and principal receivers of the phasic dopamine signal. Additionally, the basal ganglia has been posited to have a vital role in responding to different forms of stimulus salience (Zink et al., 2006; Zink et al., 2003), as well as determining which stimuli are salient (or meaningful) to the task at hand (Lidsky et al., 1985). Along these lines it has recently been suggested that modulation of the fCRP to reward expectation is dependent on the meaningfulness of the rewarding stimulus to current behaviour (Holroyd et al., 2009). Indeed, recent EEG studies have demonstrated that the amplitude of the fCRP is enhanced by a sense of responsibility over outcomes (Bellebaum et al., 2010; Li et al., 2011).

In light of the information present above, it appears that the RPE theory of the fCRP only defines one aspect of the variety of stimulus conditions eliciting the fCRP. In general, the fCRP is elicited by meaningful stimuli that inform on-going behaviour with both reward expectancy and the sense of responsibility further enhancing the fCRP response. In this thesis, the link between the fCRP and the sense of responsibility is used to investigate the role of intention for the acquisition of new voluntary actions.

1.4.3 The novelty P3: dopamine-related and separable from the fCRP

The novelty P3 has also been linked to dopamine and ACC activity (Poceta et al., 2006; Polich, 2007). As highlighted above, the novelty P3 is a subcomponent of the P3 ERP family with aspects of both the frontal P3a and posterior P3b part of the signal mediating the novelty P3 (Friedman et al., 2001). In congruence with the link to dopamine activity, the novelty P3 is thought to be associated with the brain’s evaluation of novelty (Friedman et al., 2001). Similarly to the phasic dopamine response, the novelty P3 habituates to repeated presentations of a novel stimulus (Friedman and Simpson, 1994; Kazmerski and Friedman, 1995). Given that both the fCRP and the novelty P3 have been associated with dopamine activity, a key question is whether is it possible to differentiate between the two components?

As discussed above, the fCRP is elicited by rewarding, correct, or task goal stimuli with enhancement by unexpected stimuli and stimuli that participants feel a sense of responsibility over (e.g. Hajcak et al., 2006; Holroyd et al., 2011; Holroyd et al., 2008; Li et al., 2011). Comparatively, the novelty P3 is typically elicited by novel or distracter stimuli (Friedman et al., 2001; Polich, 2007) with novel stimuli that do not
match action-outcome associations further enhancing the novelty P3 (Nitto, 2006; Waszak and Herwig, 2007). Additionally, it has been suggested that differential response of the novelty P3 to task-switch stimulus demonstrates that the novelty P3 has a role in “updating task set information for goal-directed action selection” (Barcelo et al., 2006 p. 1734). Thus, to a certain degree the fCRP and novelty P3 have different psychological underpinnings that allow for their separation with appropriate task manipulations. For example, a key question in this thesis revolves around the association between brain activity and the learning of a new voluntary action. Initially during learning, a stimulus produced by the participant (sense of responsibility) is novel (participant does not know how it is produced). Thus, it would be expected that both the fCRP and the novelty P3 would be present. In order to tease apart the contributions of the two components, it would be necessary to have other conditions that manipulate aspects of responsibility and novelty.

Additionally, it is possible that the fCRP and the novelty P3 can be differentiated based on their temporal occurrence in the ERP waveform, as well as their scalp distributions. The fCRP is typically measured as the positive component of a difference wave computed from positive and negative feedback, peaking approximately 250 ms post-stimulus over frontal-central regions of the scalp and commonly measured at the FCz electrode (Holroyd et al., 2011; Holroyd et al., 2008). However, there are previous studies that have assessed the fCRP without computation of a difference wave (Hajcak et al., 2006; Holroyd et al., 2006). As highlighted above, these physical features are similar to the P2a component reported elsewhere (Potts et al., 2006; Potts, 2004). Compared to the fCRP, the novelty P3 peaks approximately 300 ms post-stimulus over central regions of the scalp, reaching maximal amplitude typically at the Cz electrode (Conroy and Polich, 2007).

1.5 Parkinson’s disease: Disrupted basal ganglia signalling

As highlighted above, the basal ganglia play a vital role in adaptive behaviour. In Parkinson’s disease (PD) the loss of normal dopamine activity within the basal ganglia disrupts adaptive behaviour. PD is an idiopathic neurodegenerative disease with the progressive death of dopamine neurons in the basal ganglia as the primary pathology. In the early stages of PD, the symptoms are predominately movement-related, with tremor, rigidity, slowness of movement, and impeded gait commonly
observed (Marsden, 1982). Impairments in cognitive and affective domains are also characteristic of early PD, though to a lesser extent. As the disease progresses, cognitive and affective impairments become more pronounced, and movement becomes severely restricted.

A recent review has proposed that persons with PD are constantly operating under goal-directed control (Redgrave et al., 2010). Striatal dopamine loss in early PD predominately occurs in the dorsal and posterior striatum (Bernheimer et al., 1973; Frey et al., 1996; Kish et al., 1988). The loss of dopamine innervation to these striatal regions results in dysfunction of the sensorimotor corticostriatal loop evident in movement-related symptoms (for a review see Redgrave et al., 2010). Conversely, dopamine innervation of the striatal regions that mediate the associative corticostriatal loop are relatively intact in early PD (Redgrave et al., 2010). The sensorimotor loop is thought to be responsible for habitual control, while goal-directed control is mediated by the associative loop (for a review see Balleine and O'Doherty, 2009). The diminished expression of automatic movements including speech, gait, blinking, and facial expression are regularly observed in early PD (Marsden, 1982). Without normal dopamine activity within the striatum, there is an abnormal increase in inhibitory signals from the basal ganglia via the thalamus to the motor cortical regions responsible for these motor behaviours (DeLong and Wichmann, 2007; Obeso et al., 2008). Additionally, individuals with PD have difficulties acquiring automatic response despite prolonged practice (Knowlton et al., 1996; Wu et al., 2010).

This disruption of the habitual mode of movement results in a proposed increased reliance on a goal-directed control of movement, requiring increased attention and cognitive effort to perform simple movements (Redgrave et al., 2010; Schneider and Chein, 2003). The notion of an increased cognitive load has been supported by studies demonstrating that PD patients have dual-task performance (e.g. Benecke et al., 1986; Brown and Marsden, 1991; Canning, 2005; Schwab et al., 1954), slowed task-set switching (e.g. Shook et al., 2005; Woodward et al., 2002), and executive dysfunction (e.g. Brown and Marsden, 1990; Dubois and Pillon, 1996; Rodriguez-Oroz et al., 2009). Additionally, reliance on the effortful, goal-directed mode of movement should result in the slowing of movement and disruption of movement by distracters. As described by Redgrave et al. (2010) “[PD] patients require
a conscious decision to start walking and they stop abruptly if they are distracted by a
different external stimulus, a new idea or another behaviour” (p. 766). Thus, because of
an increased reliance on goal-directed control, individuals with PD would constantly
have to monitor their movements and movement-outcomes. This monitoring may be
enhanced by dopamine medication used to treat motor impairments.

Since 1967 levodopa (L-Dopa) medication has been used to restore movement-
related function in PD (Cotzias et al., 1967). L-Dopa therapy ameliorates movement-
related symptoms of PD by elevating the level of dopamine in the brain (Maruyama et
al., 1996). As a result, L-Dopa therapy restores dopamine levels within the
sensorimotor loop, and thus restores plasticity to loops involving the motor cortex
(Morgante et al., 2006). However, elevating dopamine levels may adversely affect
corticostratial loops and mesocortical dopamine projections that are still relatively
intact in PD (Gotham et al., 1988). This dopamine-overdose hypothesis has been
supported by numerous studies (e.g. Cools et al., 2001; Frank et al., 2004; Moustafa et
al., 2008; Swainson et al., 2000).

With regards to outcome monitoring, Frank, Seeberger, and O’Reilly (2004)
have shown that persons with PD ON dopamine medication have an enhanced
sensitivity to positive stimuli and decreased sensitivity to negative stimuli in
comparison to when they are OFF medication. This bias towards positive feedback
while ON dopamine medication has been shown to enhance learning from positive
feedback (Rutledge et al., 2009). It has also been proposed to contribute to medication-
induced pathological gambling in PD (Avanzi et al., 2006; Dodd et al., 2005; Molina et
al., 2000) by heightening associations between betting behaviour and winning
outcomes (Pessiglione et al., 2006; Voon et al., 2010). However, the effect appears to
extend beyond positive outcomes. Moustafa, Sherman, and Frank (2008) found that
dopamine medication impaired patients’ ability to ignore distracting stimuli during a
working memory task. Along these lines, it has been suggested that medicated
individuals with PD may have an exaggerated bottom-up and/or attenuated top-down
control (Cools et al., 2010). This may underlie the finding that there is an enhanced
action-effect binding when patients with PD were ON dopamine medication, and
possibly an altered sense of agency (Moore et al., 2010a).
Evidence from the studies described above suggests that dopamine-medicated individuals with PD have an altered outcome-monitoring system. In fact, Falkenstein et al. (2001) found that medicated individuals with PD have a reduced response ERN compared to normal controls. Therefore, in this thesis outcome-related ERPs were recorded in medicated individuals with PD during various movement tasks.

1.6 Outcome monitoring and the sense of agency

Agency is the fundamental experience of control over our voluntary movements and the resulting sensory outcomes. This sense of agency underlies all voluntary movements, and is separate from the sense of ownership over both voluntary and involuntary body movements (Gallagher, 2000). Agency allows us to distinguish sensory outcomes caused by our own movements from sensory outcomes produced by external sources. As a result, the sense of agency arises from anticipation and monitoring of the outcomes of our movements (Haggard and Tsakiris, 2009).

Outcome monitoring and evaluation play a part in all the different accounts of agency. It has been proposed that agency depends on a predictive link between intentional movements and sensory outcomes (Haggard, 2005; Haggard and Clark, 2003; Haggard and Tsakiris, 2009). Sensory prediction is essential to computational models of motor control (e.g. Wolpert et al., 1995). In these models, agency is the result of a match between the sensory prediction (generated by an internal forward model based on internal motoric signals) and the actual sensory outcome (Berti et al., 2005; Blakemore et al., 2002). When there is incongruence between the predicted and actual sensory outcome, the sensory outcome is attributed to an external source. EEG studies demonstrating that the amplitude of the P3 is enhanced by unanticipated sensory outcomes following a voluntary response highlight that the novelty P3 may be a neural indicator of this incongruence (Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007).

However, there are cases in which incongruence between predicted and actual outcomes still leads to self-attribution (for a review see Synofzik et al., 2008a). One such case would be during movement-outcome learning, in which the occurrence of a sensory outcome would not be fully anticipated by the performed voluntary movement. In this case of trial-by-trial learning, when the occurrence of the sensory outcome
differs from the prediction, the prediction would be recalibrated rather than attributing the sensory outcome to an external source (Synofzik et al., 2006).

Alternative to the internal comparator account, agency has been proposed to be an inferential reconstruction based on external and situational cues (e.g. Wegner, 2003; Wegner et al., 2004). A review by Wegner (2003) emphasises the role of inference in concluding that our actions have caused external outcomes, highlighting that the sense of agency can be fallible. Indeed, previous studies have demonstrated that modifying the content of conscious thought with movement-related information or outcome-related information can modulate the sense of agency (Moore et al., 2009; Wegner et al., 2004). Separating these two accounts is a distinction between non-conceptual internal and external sensory comparisons, and conceptual representations of external and situational cues that lead to the inference of agency. Multifactorial and multilevel models of the sense of agency (e.g. Synofzik et al., 2008a; Wegner and Sparrow, 2004) reconcile these two accounts by suggesting that the sense of agency can be divided into the feeling of agency and the judgment of agency.

The feeling of agency is the implicit, non-conceptual experience of being an agent (Newen and Bartels, 2007; Synofzik et al., 2008b; Vosgerau, 2007). This lower level of agency is characterized by quick unconscious processing of sensorimotor information (David et al., 2008). As a result, the primary authorship cues are sensorimotor related (Synofzik et al., 2008a, b). At this level, neither self nor external attributions can be made (Synofzik et al., 2008b). Additionally, for tasks with an explicit goal it has been proposed that the feeling of agency would be dependent on the degree of association between the performed movements and the task goal (Synofzik et al., 2008a).

In contrast to the feeling of agency, the judgment of agency is the explicit, conceptual judgment of one's movements causing the sensory outcome (Synofzik et al., 2008b). This judgment of agency can arise from ‘feeling of agency’ input (Synofzik et al., 2008a). However, lacking the feeling of agency, higher order representations and authorship cues such as background beliefs, intentions, thoughts and contextual cues can be used to overcome sensory discrepancies (that normally mitigate the feeling of agency) to make self-attributions (Synofzik et al., 2008a, b; Wegner and Sparrow,
Additionally, the judgment of agency has been proposed to rely on the additional cognitive processing of movement-outcomes (Synofzik et al., 2008a).

When investigating the relationship between outcome monitoring and the sense of agency, it is important to consider how the performance of a voluntary movement alters the perception of outcomes. The performance of a voluntary movement has been shown to shift the perceived time of movement forward towards the proceeding outcome, while shifting the perceived time of the outcome backwards towards the preceding movement (Haggard et al., 2002). Additionally, voluntary responses enhance cortical activity to unanticipated outcomes (Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007), and performance of a movement enhances the performance monitoring of the subsequent outcome (Zhou et al., 2010).

It is not just the actual performance of the movement that alters outcome monitoring, but the intention to move. Moore, Wegner, and Haggard (2009) induced a sense of agency through the use of a supraliminal prime that corresponded with the outcome of the subsequent voluntary or involuntary movement. It was proposed that the external cue modified the content of conscious thought prior to movement, thus potentially inducing the experience of intentionally initiating movements. Indeed, a recent ERP study has demonstrated that informing participants that a task has “controllable” or “uncontrollable” outcomes can modify the fERN (Li et al., 2011). Furthermore, it has been suggested that the top-down perceptions of the task or context requirements modulate the amount of attention allocated to bottom-up processes for outcome monitoring (Synofzik et al., 2008b). In conclusion, the subject of agency is ripe for investigations into the relationship between outcome monitoring and the sense of agency. Thus, an electrophysiological understanding of how anticipation and monitoring of the outcomes of voluntary movements is essential for determining the neural basis of agency.

1.7 Thesis outline

This introduction has outlined the theoretical motivations behind the primary aspects of this investigation into the cognitive processes that govern the formation of movement heuristics. Chapter 2 presents experiments for the initial identification of the relationship between outcome-related ERPs and movement heuristics. In the first experiment of Chapter 2 the learning of a movement heuristic is compared with using
movement heuristics. The second experiment highlights differences between learning a movement heuristic to elicit a sensory outcome and responding to a sensory outcome. In Chapter 3, an investigation of abnormal dopaminergic activity in medicated individuals with Parkinson’s disease highlights how enhanced outcome evaluation and altered performance monitoring can lead to a heightened sense of control. To further investigate the sense of control, Chapter 4 examines how the interplay between cognitive processes of anticipation and monitoring correlates with judgments of agency. Each of the experimental chapters was written in the style of an independent paper. In conclusion, Chapter 5, the general discussion, provides a theoretical summary of experimental findings, and calls attention to key concepts and future considerations. All references are compiled in one section following this final chapter.
Chapter 2: Creating a movement heuristic for voluntary action: Electrophysiological correlates of ideomotor learning
Chapter 2
Creating a movement heuristic for voluntary action: Electrophysiological correlates of ideomotor learning

2.1 Abstract

Performance of voluntary behaviour requires the selection of appropriate movements to attain a desired goal. The selection of voluntary movements was proposed to be contingent on the formation of a movement heuristic or set of internal rules governing movement selection. Event-related potentials were used to identify the electrophysiological correlates of the formation of movement heuristics during ideomotor learning. In two experiments, ERPs from non-learning control tasks were compared to a movement-learning task in which a movement heuristic was formed. Novelty P3 amplitude was negatively correlated with improved performance in the movement-learning task. Additionally, enhancement of novelty P3 amplitude was observed during ideomotor learning even after controlling for attentional and inter-stimulus interval parameters. The feedback correct-related positivity (fCRP) was only elicited by sensory effects following intentional movements, the amplitude of which was enhanced when the sensory effect was the only source of performance feedback. These findings extend previous studies demonstrating the role of the fCRP in performance monitoring and the role of the P3 in learning. The present study highlights an integrative role of the fCRP and the novelty P3 for the acquisition of movement heuristics. While the fCRP indicates that the goal of intentional movements has been attained, the novelty P3 engages stimulus-driven attentional mechanisms to determine the primary aspects of movement and context required to elicit the sensory effect.
2.2 General Introduction

Human behaviour is effect-oriented; we perform many different types of movements to obtain and respond to a variety of sensory consequences. As a result, the consequences of voluntary behaviour are closely monitored and evaluated for future learning (Haggard, 2005). To decide which movements should be selected, it is necessary to acquire a set of efficient rules or a heuristic linking movements and sensory outcomes. We propose that through this close monitoring and evaluation of movement-related outcomes, movement heuristics are acquired to guide voluntary behaviour.

The notion of movement heuristics stems from the ideomotor theory. The basic tenet of the ideomotor theory is that goals control movements. The selection of a particular movement or sequence of movements is controlled by the representation of the anticipated effect (Elsner and Hommel, 2001; Greenwald, 1970a). Studies within the framework of ideomotor theory have found that the effects produced by a movement, rather than the specific movement characteristics involved, determine its selection (e.g. Aschersleben and Prinz, 1995; Greenwald, 1970b; Hommel, 1993). For example, Hommel (1993) found that the spatial location of the effect determines stimulus-response compatibility, not the spatial location of the response.

Ideomotor learning is the discovery of contingencies between effects and their eliciting movements (Elsner and Hommel, 2001, 2004). During learning, movements are carried out in an exploratory fashion and effects are perceived and registered (Elsner and Hommel, 2001; Harless, 1861; Lotze, 1852). Movements and effects that consistently occur together with tight temporal contiguity are associated together (Elsner and Hommel, 2004). This association process has been proposed to be automatic because the consistent temporal overlap between the motor pattern of a movement and the sensory pattern of the perceived effect is sufficient (Elsner and Hommel, 2001; Hommel et al., 2003). This automatic association process has been suggested to take place within the basal ganglia, where a dopamine signal elicited by the unexpected sensory effect would reinforce/strengthen the efference copy of the descending motor pattern with the afference copy of the effect’s sensory pattern (Redgrave and Gurney, 2006).
Ideomotor learning may appear automatic when the learning of a movement heuristic is relatively simple, as in the acquisition phases used by Elsner and Hommel (2001) where the association between a single key-press response and single tone is explicit. However, ideomotor learning does not always involve learning the specific mechanics of a simple movement. Instead, gleaning the principal aspects of the movement(s) eliciting a sensory effect forms a movement heuristic. This may include the specific mechanics of a movement, but also the end location of a movement, how or when a movement is performed, the sequence of movements, or any other parameters or combination of parameters that are consistently co-occurring with the effect. Recent EEG studies have shown that unanticipated effects elicited by voluntary responses enhance the amplitude of an ERP associated with outcome evaluation (Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007). Thus, it is likely that stimulus-driven outcome evaluation processes are engaged when learning a movement heuristic.

Evaluative processes necessary for acquiring movement heuristics may occur in the anterior cingulate cortex (ACC). There is accumulating evidence that the ACC is part of a frontal network involved in evaluating the outcomes of choices, and integrating outcomes over time to guide future behaviour (e.g. Rudebeck et al., 2008; Rushworth et al., 2009; Walton et al., 2007). The feedback correct-related positivity (fCRP) and the P3 are two ERPs associated with outcome monitoring and evaluation processes of the ACC (Holroyd et al., 2008; Polich, 2007; Zhou et al., 2010).

During ideomotor learning, perceived effects engage evaluative processes necessary for acquiring a movement heuristic. The evaluation of a sensory effect begins when it is initially unexpected, eliciting an orienting response that is indexed by the novelty P3 (for a review see Friedman et al., 2001). The novelty P3, which occurs approximately 300 msec following a novel or unexpected event, is associated with evaluation of novel unexpected effects (Friedman et al., 2001). Importantly, the amplitude of the novelty P3 demonstrates plasticity in that it reduces in amplitude with repeated presentations of the unexpected or novel stimulus (Courchesne et al., 1975; Friedman and Simpson, 1994; Kazmerski and Friedman, 1995). The habituation of the novelty P3 is proposed to indicate that its underlying neural mechanisms facilitate the formation of a new neural representation so that the novel stimulus is no longer
unexpected (Friedman et al., 2001). Recently it has been shown that the unique information conveyed by a surprising stimulus determines the trial-by-trial activity of attentional mechanisms underlying the generation of the P3 (Mars et al., 2008). Unexpected effects produced by voluntary movements would also convey movement related information (via the basal ganglia as highlighted above).

The novelty P3 is a specific instance of the ubiquitous P3 component that is implicated in the evaluation of both positive (e.g. Hajcak et al., 2005; Zhou et al., 2010) and negative outcomes (Falkenstein et al., 1999; Nieuwenhuis et al., 2001; Overbeek et al., 2005; Ridderinkhof et al., 2009). Further, previous studies have demonstrated the unique role of the P3 in learning (e.g. Groen et al., 2007; Jongsma et al., 2006; Lindin et al., 2004; Sailer et al., 2010). Specifically, in Sailer et al. (2010) only the P3 amplitude in learners showed significant reductions from a pre-learning phase to a post-learning phase. This reduction was not found in non-learners. Also, P3 amplitude was found to be a valid predictor of task performance. Therefore, P3 amplitude, specifically novelty P3 amplitude, appears to be a persuasive index of learning a movement heuristic. In fact, previously it was suggested that the P3 reflects the updating of an internal model of the movement environment (Krigolson et al., 2008). Novelty P3 amplitude would be related to the amount of stimulus-driven attentional processes required for gleaning primary aspects of movement and contextual information necessary for acquiring a movement heuristic.

The fCRP is another useful indicator of monitoring the consequences of voluntary behaviour. In particular, the fCRP is a positive waveform occurring 200-300 msec post-stimulus, which has been proposed to index the achievement of task goals (Hajcak et al., 2006; Holroyd et al., 2008). While the feedback error-related negativity (fERN, also referred to as feedback related negativity) is commonly used as an index of outcome monitoring, evidence from previous studies suggests that fERN amplitude is more affected by positive or correct feedback than by negative or error feedback (Eppinger et al., 2008; Hewig et al., 2008; Holroyd et al., 2008; Potts et al., 2006). Along these lines, the fCRP was proposed by Holroyd, Pakzad-Vaezi, and Krigoloson (2008) to account for the modulation of the fERN by positive or correct feedback.

Prior to the proposal of Holroyd, Pakzad-Vaezi, and Krigoloson (2008), the fCRP has been referred to as the P2a, P3f, frontal polar component, or frontal selection
positivity (Kenemans et al., 1993; Makeig et al., 1999; Potts et al., 1996; Potts and Tucker, 2001). These previous studies highlight the role of the fCRP in indexing the occurrence of task- or behaviourally-relevant stimuli (Potts et al., 2006; Potts, 2004; Potts et al., 1996). Additionally, recent studies have demonstrated greater modulation of the fERN for outcomes linked to voluntary behaviour (Bellebaum et al., 2010; Zhou et al., 2010). Based on these collective studies, we proposed that the fCRP would be a practical indicator of the sensory outcomes related to voluntary behaviour.

The aim of the present study was to investigate whether ERPs associated with outcome evaluation are engaged during ideomotor learning of a movement heuristic. To this aim, a movement-learning task was developed in which participants were instructed to elicit a certain sensory effect but they were not told how. In this task, the movement heuristic required to produce the sensory effect was the end location of the participants’ movements. Ideomotor learning was investigated in two experiments. In Experiment 1, we attempted to elucidate the ERP(s) particular to learning the movement heuristic. Experiment 2 was then conducted to investigate the ERP(s) necessary for monitoring the outcomes in order to learn the movement heuristic.

2.3 Experiment 1

In Experiment 1, ERPs from the movement-learning task were compared to non-learning movement tasks in which the movement heuristic was pre-defined. The movement heuristic employed to elicit the sensory effect was similar across all tasks. Attaining the sensory effect was dependent on the end location of the participants’ movements. However, information provided to the participants at the beginning of each task varied. In the movement-learning task participants were not instructed how to elicit the sensory effect. In the two non-learning tasks participants were either shown a location prior to the start of the task or the location was visible during the duration of the task. It was hypothesized that only the learning task would elicit a novelty P3 that would reduce with learning of the movement heuristic. This is due to the fact that stimulus-driven attentional processes would be required to acquire a movement heuristic, but as a movement heuristic is developed, the reliance on processes that underlie acquisition of the movement heuristic will decrease. In the non-learning tasks, information regarding how to elicit the sensory effect is provided at the beginning or during the task. As a result, stimulus-driven attentional processes underlying the
novelty P3 will not be engaged. Given that participants’ movements elicited the sensory outcome across all tasks, it was hypothesized that no difference in fCRP would be observed.

### 2.3.1 Methods

**Participants**

The participants in Experiment 1 were 12 students (5 males), aged 20-26 (mean age 23 years) from the University of Otago. All participants were reimbursed NZ$ 25 to compensate for their time. Prior to the experiment, they were given an information sheet and informed consent was obtained. The Lower South Otago Regional Ethics Committee approved all procedures.

**Stimuli**

The stimulus representing the sensory effect was a green circle (2.02° visual angle) presented in the centre of the screen over a central grey fixation cross (0.4°) for 100 msec. The cursor was a grey circle (0.4°) controlled by a tracking-ball mouse. A grey outline of a circle (2.02°) was used in the two non-learning tasks in Experiment 1 to define the specific location (hot spot) on the screen that would elicit the sensory effect when the cursor was moved to the hot spot. The size of the hot spot was the same in the movement-learning task; however no visual stimulus was presented to define the hot spot (i.e. the hotspot was not visible to the participant). All visual stimuli were presented against a black background on a 54cm display. MatLab software (MathWorks, Inc., vR2008a) was used for all stimulus presentation and collection of behavioural responses.
Figure 2.1 A schematic illustration of the movement-learning task (A), the continuous-cue task (B), and the initial-cue task (C) of Experiment 1. The pre-task screen was presented until the participant was ready. Then, participants moved the cursor on the screen to elicit the green circle. When the cursor was moved into the ‘hot spot’ the green circle was presented for 100 msec. The cursor was then reset and participants repeated the actions to elicit the green circle. Dashed-line circle indicates the location of the ‘hot spot’ when it was not visible to the participant.
Experimental procedures

In Experiment 1, participants were informed that their goal was to cause green circles to appear on the screen. They were instructed to use the tracking-ball mouse to move the cursor on the screen to elicit green circles, and that the green circles would always be presented directly over the centrally positioned fixation cross. They were further instructed to look at the fixation cross throughout the trials. During the movement-learning task, participants were not given any specific instructions about how to elicit the green circle, and they were told that they would learn over the course of the experiment.

A schematic illustration of the movement-learning task and the non-learning tasks are presented in Figure 2.1. In the movement-learning task, a green circle was presented when the cursor was moved to within the area of the hot spot (Figure 2.1A). After each presentation of the green circle the cursor was re-positioned to a random starting location on the screen to initiate the same process of learning once again. The purpose of re-positioning the cursor was so that final position (endpoint), and not the initial position of the movement, was the critical determinant of eliciting the presentation of the green circle. The participants were then to repeat the movements required to again elicit a green circle. The hot spot remained constant over the course of a block, but was in a different (randomly-determined) location on each of the three blocks. Each block ended after 30 presentations of the green circle.

At the start of the first non-learning task (continuous-cue), the participants were instructed to elicit the green circle by moving the cursor into the location defined by a grey outline of a circle on the screen (i.e. the hotspot was directly present to the participants; Figure 2.1B). In the second non-learning task (initial-cue) the grey outline of a circle was presented at the start of the trial only, to cue a specific location (i.e. the hot spot was presented and then removed, with the expectation that participants would remember where it was; Figure 2.1C). For the initial-cue task, the participants were instructed that as soon as the block began the cue would be removed, and that moving the cursor to the location on the screen defined by the cue would elicit the green circle. Similar to the movement-learning task, for both non-learning tasks, the cursor was re-positioned to a different location on the screen following each presentation of the green
circle, the location of the hot spot remained constant over the course of a block and varied across blocks, and a block ended after 30 presentations of the green circle. In Experiment 1, a total of nine blocks were conducted, with one block of the continuous-cue task and one block of the initial-cue task following each of the three blocks of the movement-learning task in a counterbalanced design (i.e. ABC-ABC-ABC or ACB-ACB-ACB).

**EEG data acquisition**

Electroencephalography (EEG) and electrooculography (EOG) data were collected continuously using a 32-channel Ag-Ag/Cl sintered Quickcap and a Neuroscan Synamps amplifier, interfaced with a Dell Intel computer running Scan 4.3 software. Data were sampled at 1000Hz with a band pass of 0.5–200Hz, and gain was ×500. The 28 scalp electrode sites were referenced to linked mastoid electrodes, with AFz as the ground. Horizontal EOG data were recorded from two electrodes placed on the outer canthi of the two eyes. Vertical EOG data were recorded from linked electrodes on the infraorbital and supraorbital ridges of the left eye. Impedances were maintained below 5kΩ.

**2.3.2 Data analysis**

**Behavioural analysis**

For the movement-learning task and the two non-learning tasks, the time it took the participants to elicit each green circle was recorded. These times were used to determine hit rate, or the number of green circles presented per 2 sec interval. The hit rate was used as a behavioural measure of the formation of a movement heuristic and was calculated for the first half of green circle occurrences (1–15; F15) and second half of green circle occurrences (16–30; L15) of each block in order to investigate changes in performance within a block.

**EEG analysis**

EEG data analysis was conducted offline using purpose-written MatLab scripts. Continuous EEG data were epoched with respect to stimulus onset (200 msec prior and 1000 msec after the green circle) in the behavioural task, and baseline corrected relative to the 200 msec period prior to stimulus onset. Prior to averaging, epochs containing ocular artefacts were removed using a ‘step function’ with a 75µv threshold (Luck,
2 ERPs of movement heuristics

Participants with fewer than 20 trials remaining following the artefact rejection process were excluded from further analysis. Of the 12 participants, 2 did not meet this criterion and were removed from EEG analysis. EEG data were then low-passed filtered (30Hz) using a phase-shift-free Butterworth filter and re-baseline corrected. The mean amplitude of the fCRP was measured at the midline FCz electrode site (located above the pre-supplementary motor area/supplementary motor area) and averaged across the time window 200–250 msec (Potts, 2004). The mean amplitude of the novelty P3 was measured at the midline Cz electrode site (located above the supplementary motor area/primary motor cortex) and averaged across the time window 300–350 msec (Jentzsch and Sommer, 2001; Polich and Comerchero, 2003). For plotting purposes EEG data were smoothed using a one-dimensional digital filter with a 25 msec time window.

Statistical analysis

Hit rates were analysed using a repeated-measures ANOVA with the within-subjects factors task (movement-learning, continuous-cue, initial-cue), block-half (F15, L15) and block (Block 1, Block 2, Block 3). Similar analyses were conducted for the mean amplitude measures of the novelty P3 and the fCRP.

To tease apart specific effects of interactions, additional repeated-measures ANOVAs and planned comparisons were used where appropriate to test our hypotheses. Effects were considered significant if \( p < .05 \). Greenhouse–Geisser corrections were applied to \( p \)-values where appropriate. Effect sizes are shown using partial eta squared (\( \eta^2 \)). All statistical tests were conducted using SPSS (version 18.0) software.

2.3.3 Results

Behavioural data

The hit rate in each task increased across blocks, and within blocks for the movement-learning task and the two non-learning tasks (Figure 2.2). Verifying these effects, significant main effects of task, \( F(2,22) = 79.89, p < .001, \eta^2 = .88 \), block-half, \( F(1,11) = 38.99, p < .001, \eta^2 = .78 \), and block, \( F(2,22) = 25.77, p < .001, \eta^2 = .70 \), were found, with no significant interactions. Pairwise comparisons for task demonstrated that the hit rate for the movement-learning task (\( M = 0.91, SE = .06 \)) was significantly
smaller than in the continuous-cue task (M = 1.93, SE = .08), p < .001, and
significantly smaller than in the initial-cue task (M = 1.85, SE = .08), p < .001.
ANOVA.s for each task with block-half and block as within-subjects factors yielded a
significant main effect of block with the hit rate increasing for each task: movement-
learning task, F(2,22) = 19.66, p < .001, η² = .64, continuous-cue task, F(2,22) = 7.57, p
= .008, η² = .41, initial-cue task, F(2,22) = 5.55, p = .016, η² = .36. Only the movement-
learning task and the continuous-cue task produced a significant main effect of block-
half, F(1,11) = 59.78, p < .001, η² = .85, and, F(1,11) = 13.89, p = .003, η² = .56,
respectively. A post-hoc paired-samples t-test showed that the change in hit rate,
collapsed across block, between first and last half of a block was significantly larger for
the movement-learning task (M = .50, SD = .46) than for continuous-cue task (M = .10,
SD = .24), t(35) = 4.44, p < .001.

Figure 2.2 The hit rate for each block-half (F15, L15) of the movement-learning task (ML), the
continuous-cue task (CC), and the initial-cue task (IC) of Experiment 1. There was a general
improvement in performance across all tasks. Compared to CC and IC the ML demonstrates
greater performance improvements within and across block. Error bars indicate standard error.
Figure 2.3 Average ERP waveforms at Cz electrode site for each block 1 (A), block 2 (B), and block 3 (C) of the movement-learning task (ML), the continuous-cue task (CC), and the initial-cue task (IC) of Experiment 1. There was a reduction of the novelty P3 across blocks of the ML. No learning-related changes were observed in the fCRP as illustrated here, and as analysed at FCz.
Figure 2.4 (A) Average ERP difference waveforms at Cz electrode site for the movement-learning task – continuous cue task (blue line), movement-learning task – initial cue task (red line), and movement-learning task block 1 – movement-learning task block 3 (green line). Scalp distributions for the 325 ms time point where the difference waves reach peak amplitude for movement-learning task – continuous cue task (B), movement-learning task – initial cue task (C), and movement-learning task block 1 – movement-learning task block 3 (D). The difference wave scalp distributions show a central distribution, consistent with observed scalp distributions for the novelty P3. Blue and red coloring represents negative and positive intensity on the scalp distribution, respectively.

fCRP results

An fCRP was elicited by all tasks in Experiment 1 (Figure 2.3). fCRP amplitude was significantly different across task, $F(2,18) = 4.83, p = .023, \eta^2 = .35$, and block-half, $F(1,9) = 7.29, p = .024, \eta^2 = .45$. Pairwise comparisons for task demonstrated that the fCRP amplitude in the movement-learning task ($M = 8.65 \mu V, SE = .73 \mu V$) was significantly larger than in the continuous-cue task ($M = 6.91 \mu V, SE = .94 \mu V$), $p = .04$. As for the significant main effect of block-half, pairwise comparisons demonstrated that the fCRP amplitude from the first half of a block ($M = 8.21 \mu V, SE = .91 \mu V$) was
significantly larger than in the second half of a block (M = 6.92 µV, SE = .83 µV), p = .024.

Novelty P3 results

Visual inspection of the ERP waveforms indicated that only the movement-learning task elicited an enhanced novelty P3 component that decreased over the course of the experiment (Figure 2.3). Additionally, difference waves and their corresponding scalp distributions isolate the novelty P3 to the movement-learning task (Figure 2.4). Verifying this, the corresponding analyses on novelty P3 amplitude yielded significant main effects of task, F(2,18) = 31.43, p < .001, η² = .78, block-half, F(1,9) = 22.29, p = .001, η² = .71, and block, F(2,18) = 6.74, p = .018, η² = .43, with significant interactions of task x block-half, F(2,18) = 5.66, p = .02, η² = .38, and task x block, F(4,36) = 4.63, p = .029, η² = .34. Pairwise comparisons for task indicated that the amplitude of the novelty P3 in the movement-learning task (M = 10.54 µV, SE = 1.36 µV) was significantly larger than in the continuous-cue task (M = 2.86 µV, SE = .48 µV), p = .001, and the initial-cue task (M = 3.53 µV, SE = .80 µV), p < .001. Pairwise comparisons for block-half demonstrated that the amplitude of the novelty P3 in the first half of a block (M = 7.1 µV, SE = .7 µV) was significantly larger than in the second half of a block (M = 4.2 µV, SE = .9 µV), p = .001. Pairwise comparisons for block indicated that amplitude of the novelty P3 produced in Block 1 (M = 7.79 µV, SE = 1.12 µV) was significantly larger than Block 2 (M = 4.89 µV, SE = .73 µV), p = .007.

ANOVA for each task with block-half and block as within-subjects factors yielded a significant main effects of block-half in the movement-learning task, F(1,9) = 33.07, p < .001, η² = .78. Pairwise comparisons for block-half demonstrated that the amplitude of the novelty P3 in the first half of a block (M = 13.18 µV, SE = 1.65 µV) was significantly larger than in the second half of a block (M = 7.90 µV, SE = 1.17 µV), p < .001. A significant main effect of block was found in the movement-learning task, F(2,18) = 5.95, p = .029, η² = .40. Pairwise comparisons for block in the movement-learning task indicated that amplitude of the novelty P3 produced in Block 1 (M = 15.25 µV, SE = 2.24 µV) was significantly larger than Block 2 (M = 8.06 µV, SE = 1.14 µV), p = .01. A significant main effect of block was also found in the initial-cue control task, F(2,18) = 9.76, p = .002, η² = .52. Pairwise comparisons for block in the initial-cue control task indicated that amplitude of the novelty P3 produced in Block
1 (M = 5.15 µV, SE = .84 µV) was significantly larger than Block 3 (M = 1.69 µV, SE = .91 µV), p = .006.

Additionally, a one-tailed Pearson correlation showed that there was a significant negative correlation between novelty P3 amplitude and hit rate for the movement-learning task, r = -.61, n = 60, p < .001.

2.3.4 Discussion: Experiment 1

The acquisition of a movement heuristic was demonstrated by the significant increase in hit rate within and across blocks of the movement-learning task. The improvement in hit rate was the result of the participants’ behaviour shifting from broad exploratory movements to efficient movements that had similar end locations. Refinement of the movement heuristic was also observed in the non-learning tasks. The non-learning tasks showed significant, but modest increases in hit rate compared to the movement-learning task. Collectively, and especially in the movement-learning task, with each occurrence of the sensory effect primary aspects of movement and contextual information were gleaned to form and refine a movement heuristic.

Similar to previous studies, the fCRP indicated that a desired sensory effect was attained (Hajcak et al., 2006; Holroyd et al., 2006; Holroyd et al., 2008). No difference in fCRP amplitude was found between the movement-learning task and the initial-cue task. In both tasks the sensory effect was the only indicator that that the goal of the participants’ movements had been achieved. However, in the continuous-cue task, feedback was also provided by the continuous cue. Therefore, participants’ dependence on the sensory effect for performance feedback was reduced. The significantly reduced fCRP amplitude observed in the continuous-cue task compared to the movement-learning task verified this. As result, fCRP amplitude may be sensitive to the degree to which a stimulus indicates that task goals have been achieved. Also it is important to note that in both the continuous cue and the initial cue tasks there is a relative reduction in meaningfulness of the stimulus given that the stimulus does not also inform subsequent learning. Thus, the degree to which the fCRP indicates that the task goal has been achieved appears to also be modulated by meaningfulness of the task goal for task performance. This would explain the lack of difference between the initial cue and the continuous cue task.
A reduction in fCRP amplitude was also observed within blocks after collapsing across all tasks. This may reflect a more general reduction in motivational significance of the sensory effect for performance monitoring (Sailer et al., 2010); as participants’ movements consistently produced the sensory effect the motivation to monitor performance diminished.

Importantly, novelty P3 amplitude correlated with the learning of a movement heuristic. The amplitude of the novelty P3 reduced with learning within blocks and across blocks of the movement-learning task. A negative correlation was also found between novelty P3 amplitude and hit rate in the movement-learning task. Only a moderate novelty P3 was elicited during the first block of the initial-cue task, indicating refinement of a movement heuristic. These findings are consistent with previous studies showing learning related changes in the P3 (e.g. Groen et al., 2007; Jongsma et al., 2006; Lindin et al., 2004; Sailer et al., 2010), as well as a functional link with movement (Krigolson et al., 2008).

However, the observed reduction in novelty P3 amplitude may also be the result of parameters that are potentially confounded with learning. The amplitude of the P3 is dependent on subjective probability, available attentional resources, cognitive effort of the task, and the inter-stimulus interval (for a review see Polich, 2007). While some of these parameters are directly affect by learning (Sailer et al. 2010), the possibility of such effects cannot be ruled out. To address these concerns, a second experiment was conducted.

2.4 Experiment 2

Experiment 2 was conducted to further investigate the role of the fCRP in performance monitoring, and to control for the observed reduction in inter-stimulus interval that occurred with learning. Performance monitoring is necessary for learning, especially for ideomotor learning in which the perceptual features of the sensory effect mediate the selection of voluntary movements (Greenwald, 1970a). To determine if performance monitoring is particularly enhanced during ideomotor learning, fCRP amplitudes from the movement-learning task and a stimulus-response task with stimulus-based movements were compared. Stimulus-based movements are movements that are under the control of externally produced stimuli. It has been suggested that
ideomotor learning only applies to voluntary or intentional-based movements, and the two modes of movement (i.e. stimulus-based and intentional-based) have different neural substrates (Herwig et al., 2007).

In the stimulus-response task conducted in Experiment 2, participants were informed that their movements did not elicit the sensory effect. However, the sensory effect was the imperative stimulus to which participants responded. As a result, the sensory effect, similar to the movement-learning task, was motivationally significant for the performance of the task. Previously, Potts (2004) found that the amplitude of the fCRP was enhanced for overt responses to a target stimulus compared to covert responses. Additionally, it has been suggested that attentional demands are similar for intentional-base and stimulus-based movements (Herwig and Waszak, 2009). Any difference in the fCRP would suggest a difference in performance monitoring for intentional-based movements compared to stimulus-based movements. Thus, a difference would extend prior evidence that intentional-based and stimulus-based movements are controlled by different neural substrates (cf. Herwig et al., 2007).

The stimulus-response task also served as a control for the reduction in the inter-stimulus interval observed with learning. The timing of the sensory effect, serving as the imperative stimulus, was based on occurrences of the sensory effects that were attained by the participants’ voluntary movements. Therefore, there was no difference in the inter-stimulus interval across the two tasks for each participant. As a result, the novelty P3 elicited by the movement-learning task and the stimulus-response task could be compared to determine the influence of the inter-stimulus interval.

It was hypothesized, based on the findings of Experiment 1 and previous studies highlighting the role of the fCRP in indexing the occurrence of task- or behaviourally-relevant stimuli (Potts et al., 2006; Potts, 2004; Potts et al., 1996), that fCRP amplitude would be larger in the movement-learning task compared to the stimulus-response task. This would be the result of an increased need to monitor the outcome of performance during the movement-learning task, which is necessary for forming and refining a movement heuristic. While monitoring is necessary in the stimulus-response task to respond to imperative stimuli, monitoring of the sensory effect is not required to supply feedback for performance.
Additionally, it was hypothesized that the novelty P3 elicited during both the movement-learning task and the stimulus-response task would reduce in amplitude as the timing of the sensory effect decreased. However, novelty P3 amplitude in the movement-learning task was hypothesized to be significantly larger than novelty P3 amplitude in the control task as a result of increased stimulus-driven attention that underlies the novelty P3. Stimulus-driven attention would increase to process movement and contextual information necessary for learning a movement heuristic.

2.4.1 Methods

Methods similar to those in Experiment 1 were used, except for the following details.

Participants

The participants were 12 students (5 males), aged 19-24 (mean age 20 years) from the University of Otago. All participants were reimbursed NZ$ 25 to compensate for their time. Prior to the experiment, they were given an information sheet and informed consent was obtained. The Lower South Otago Regional Ethics Committee approved all procedures.

Stimuli

In the stimulus-response task, there was no hot spot; timing of the presentation of the sensory effect was computer-controlled and not dependent on the specific movements of the participants.
Figure 2.5 A schematic illustration of the movement-learning task (A) and the stimulus-response task (B) of Experiment 2. The pre-task screen was presented until the participant was ready. Compared to the movement-learning task presentation of the green circle in the stimulus-response task was computer-controlled. The participant responded to the green circle by moving the cursor to the fixation cross, then continued to move the cursor in a random fashion. Dashed-line circle indicates the location of the ‘hot spot’ when it was not visible to the participant.
Experimental Procedure

A schematic illustration of the movement-learning task and the stimulus-response task are presented in Figure 2.4. Five consecutive blocks of the movement-learning task were conducted before the blocks of the stimulus-response task. The movement-learning task of Experiment 2 was performed in the same manner as in Experiment 1: the participants were not given any specific instructions about how to elicit the green circle, and they were told that they would learn over the course of the experiment. A block ended after 30 presentations of the green circle (Figure 2.4A).

Five blocks of a stimulus-response task followed the five consecutive blocks of the movement-learning task. Prior to the start of the stimulus-response task, the participants were informed that their own movements would not elicit the green circle. Rather, they were instructed to move the cursor around the screen and respond to presentation of the green circle by moving the cursor to the fixation cross and then resume moving the cursor around the screen (Figure 2.4B). The timing of the sensory effects in each of the five blocks was controlled to have the same inter-stimulus interval as the corresponding block of the movement-learning task performed by the same participant; meaning that any variation or decrease in the timing interval of the sensory effects in the movement-learning task would be directly controlled for by the stimulus-response task. A block ended after 30 presentations of the green circle.

EEG analysis

This analysis was the same as in Experiment 1. Similarly, participants with fewer than 20 trials remaining following the artefact rejection process were excluded from further analysis. Of the 12 participants, 3 did not meet this criterion and were removed from EEG analysis.

Statistical analysis

In Experiment 2, the hit rates from the movement-learning task were analysed using a repeated-measures ANOVA with the within-subjects factors block-half (F15, L15) and block (Block 1, Block 2, Block 3, Block 4, Block 5). The mean amplitude measures of the novelty P3 and the fCRP were analysed using a repeated-measures ANOVA with the factors task (movement-learning, stimulus-response), block-half (F15, L15) and block (Block 1, Block 2, Block 3, Block 4, Block 5).
2.4.2 Results

Behavioural data

The hit rate increased within each block and across blocks of the movement-learning task (Figure 2.5). The corresponding ANOVA produced significant main effects of block-half, $F(1,11) = 50.02, p < .001, \eta^2 = .82$, and block, $F(4,44) = 6.63, p = .001, \eta^2 = .38$.

![Figure 2.6](image)

*Figure 2.6* The hit rate for each block-half (F15, L15) of the movement-learning task (ML) of Experiment 2. There was a general improvement in performance within and across blocks. Error bars indicate standard error.

fCRP results

The fCRP elicited by the movement-learning task was larger than the fCRP elicited by the stimulus-response task (Figure 2.7). There was a significant main effect of task on fCRP amplitude, $F(2,18) = 18.72, p = .003, \eta^2 = .70$. Pairwise comparisons for task demonstrated that the fCRP amplitude from the movement-learning task ($M = 8.79 \mu V, SE = 1.81 \mu V$) was significantly larger than in the stimulus-response task ($M = 3.92 \mu V, SE = 1.59 \mu V$), $p = .003$. This fCRP difference between the two tasks is highlighted by a difference wave (Figure 2.8B) computed from the difference wave of movement-learning task – stimulus-response task and the difference wave of the first
block-half of the movement-learning task – the last block-half of the movement-learning task (Figure 2.8A).

**Novelty P3 results**

In Experiment 2, both the movement-learning task and the stimulus-response task produced novelty P3 waveforms (Figure 2.7). Results from the corresponding ANOVA produced significant main effects of task, $F(1,8) = 19.77$, $p = .002$, $\eta^2 = .71$, block-half, $F(1,8) = 39.39$, $p < .001$, $\eta^2 = .83$, and block, $F(4,32) = 5.08$, $p = .01$, $\eta^2 = .39$. Pairwise comparisons for task demonstrated that the amplitude of the novelty P3 in the movement-learning task ($M = 13.02 \mu V$, $SE = 1.42 \mu V$) was significantly larger than in the stimulus-response task ($M = 8.2 \mu V$, $SE = 1.08 \mu V$), $p = .002$. Pairwise comparisons for block-half revealed that the amplitude of the novelty P3 in the first half of a block ($M = 12.63 \mu V$, $SE = 1.30 \mu V$) was significantly larger than the amplitude of the novelty P3 in the second half of a block ($M = 8.61 \mu V$, $SE = 1.05 \mu V$), $p < .001$.

ANOVA for each task with block-half and block as within-subjects factors yielded main effects of block-half, $F(1,8) = 20.11$, $p = .002$, $\eta^2 = .72$, and $F(1,8) = 83.93$, $p < .001$, $\eta^2 = .91$, and block, $F(4,32) = 3.43$, $p = .038$, $\eta^2 = .30$, and $F(4,32) = 3.05$, $p = .03$, $\eta^2 = .28$ for the movement-learning task and the stimulus-response task, respectively.

One-tailed Pearson correlations showed a significant negative correlation between novelty P3 amplitude and hit rate for both the movement-learning task, $r = -.54$, $n = 100$, $p < .001$, and the stimulus-response task, $r = -.51$, $n = 100$, $p < .001$ (Figure 2.7B-C)
Figure 2.7 Average ERP response to the sensory event at Cz electrode site. (A) Sensory outcomes during the movement-learning task (ML) elicited a larger fCRP and novelty P3 compared to during the stimulus-response task (SR). The novelty P3 from both (B) the ML and (B) the SR demonstrated a significant negative correlation between task improvement measured from the ML, highlighting that reduction in novelty P3 amplitude is associated with a reduction in the inter-stimulus interval.
Figure 2.8 (A) Average ERP difference waveforms at Cz electrode site for movement-learning task – stimulus-response task (red line) and movement-learning task first block-half – movement-learning task last block-half (blue line). (B) The difference wave (green line) produced from the subtraction of the ML – SR difference wave and the ML F15 – ML L15 difference wave and the resulting scalp distributions for the 225 ms time point where the difference wave reached peak amplitude. The difference wave scalp distribution shows a fronto-central distribution, consistent with observed scalp distributions for the fCRP. Blue and red coloring represents negative and positive intensity on the scalp distribution, respectively.
2.4.3 Discussion: Experiment 2

Performance monitoring, as indicated by the amplitude of the fCRP, was enhanced during the movement-learning task compared to the stimulus-response task. fCRP amplitude in the learning task was significantly larger than fCRP amplitude in the control task. This suggests that heightened performance monitoring (i.e. the indication that a desired goal has been attained) has a contributory role in the learning of a movement heuristic. However, unlike Experiment 1, no significant reduction in fCRP amplitude was observed within or across blocks of the movement-learning task or the stimulus-response task. This indicates that the motivational significance of the sensory effect did not change with learning or reductions in the inter-stimulus interval.

Stimulus-driven attention was increased for learning a movement heuristic independent of a decreasing inter-stimulus interval. Novelty P3 amplitude was significantly larger in the movement-learning task compared to novelty P3 amplitude in the stimulus-response task and there was no difference between the tasks in the inter-stimulus interval of the sensory effect. Thus, any difference was not the result of sensory effect timing.

However, the ability to allocate attention to the sensory effect was also influenced by the decreasing inter-stimulus interval (Fitzgerald and Picton, 1984; Gonsalvez et al., 2007; Gonsalvez and Polich, 2002; Pashler, 1994; Polich, 2007). Both tasks showed reductions in novelty P3 amplitude that correlated with improved hit rate in the movement-learning task. This suggests that the observed reduction in novelty P3 amplitude was partially determined by the reduction in inter-stimulus interval that was the result of improved performance on the movement-learning task.

2.5 General Discussion

In the present study, the aim was to investigate whether ERPs associated with outcome evaluation were engaged during ideomotor learning of a movement heuristic. To investigate the acquisition of a movement heuristic a novel movement-learning task was developed. In the movement-learning task, participants were instructed that the goal of the task was to elicit a certain sensory effect but they were not informed how. As a result, the movement heuristic for attaining the desired sensory effect was unknown to the participants at the start of the task. Using a similar approach to the one
commonly used in animal operant-learning studies as a measure of learning, the hit rate was used as a behavioural measure of movement heuristic formation. The acquisition of a movement heuristic would shift the participants’ movements from broad exploratory movements to efficient movements that consistently result in the presentation of the sensory effect.

In both experiments, the hit rate in the movement-learning task significantly increased within each block and across blocks. In Experiment 1, the two non-learning tasks also showed moderate but significant improvements in hit rate within and across blocks. As concluded above, these behavioural findings suggest that the participants formed and refined a movement heuristic for quick and efficient goal achievement. In accordance with the ideomotor theory, the formation of a movement heuristic was controlled by the goal of the participants’ movement. In the movement-learning task employed in this study, the desired sensory effect was the required end location of the participants’ cursor movements. Therefore, because there was more than one method possible to reach the end location, learning how to produce the sensory effect was not a simple (potentially automatic) movement-to-effect association employed by previous studies (e.g. Elsner and Hommel, 2001, 2004). After learning, participants engaged movements that ended in a specific location, irrespective of the start position on each trial. Thus, specific motor characteristics did not determine the selection of the movements the participants employed. Rather, it was the utility of the movement to reach a specific location that mattered.

2.5.1 The Novelty P3: Evaluation of unanticipated sensory outcome to update the movement heuristic

Enhancements in novelty P3 amplitude were observed during ideomotor learning even after controlling for attentional and inter-stimulus interval parameters. Similar to previous P3 learning studies, it was found that with improved task performance there was a significantly correlated reduction in novelty P3 amplitude (e.g. Sailer et al., 2010). Using the stimulus-response task with temporally equivalent occurrences of the sensory effect and heightened attention, the present study extended these findings and more clearly demonstrate the use of P3 as a measure of learning. Additionally, our results shed light onto recent research that has shown an enhancement in novelty P3 amplitude following unanticipated effects elicited by voluntary responses
(Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007). The novelty P3 elicited in our study, and in these previous studies, reflects the engagement of attentional mechanisms necessary for gleaning primary aspects of movement and contextual information necessary for understanding the cause of the unanticipated effect. Overtime, the reoccurrence of the novelty P3 would provide sufficient information for learning a movement heuristic.

The role of the P3 in facilitating the formation of an accurate movement heuristic is implicated in its function to update current mental schemata (or heuristics) as proposed by the context updating theory (Donchin and Coles, 1988). Similarly, the P3 has previously been proposed to reflect the updating of internal models of the movement environment (Krigolson et al., 2008). Our findings fit with and extend the updating role that the P3 has in guiding future movements. A previous study conducted by Mars et al. (2008) used trial-by-trial analysis of the P3 to demonstrate that the unique information conveyed by a surprising stimulus determines P3 amplitudes. A similar process may underlie the present results. With each presentation of the sensory effect, recent movement and contextual information converges in cortical areas. Stimulus-driven attentional processes underlying the novelty P3 are engaged to determine the primary aspects of movement and contextual information. As these primary aspects are gleaned to form a movement heuristic, the unique information conveyed by the sensory effect reduces, which in turn results in a reduction of the required attentional processes and the resultant novelty P3.

2.5.2 The fCRP: Goal attainment and movement-outcome coupling

The fERN/fCRP have been proposed to respond to outcomes in a binary fashion: the task goal has been achieved or it has not (Hajcak et al., 2006; Holroyd et al., 2006; Holroyd et al., 2008). In this vein, the results in Experiment 1 demonstrated that all tasks elicited a robust fCRP, because in all tasks the sensory effect indicated that the task goal had been achieved. However, in the continuous-cue task, the continuous cue also provided feedback regarding achievement of the task goal. As a result, fCRP amplitude in the continuous-cue task was found to be significantly smaller than fCRP amplitude in the movement-learning task. It has been suggested that the fCRP is modulated by the task or behavioural-relevance of stimulus (Potts, 2004; Potts et al., 1996). Along these lines, fCRP amplitude appears to be sensitive to the degree to
which the sensory outcome indicates that task goals have been achieved, as well as the meaningfulness of the goal to for task performance.

fCRP amplitude was enhanced by sensory outcomes produced by intentional-based movements compared to the sensory effects that were the imperative stimuli in stimulus-based movements. The waveform elicited during the stimulus-response task, in Experiment 2, was similar in appearance to the waveform elicited by the target stimulus in an oddball task, in which a P2a precedes the P3 component (Potts et al., 1996). In fact, the stimulus-response task was performed in a similar manner to a single-stimulus oddball task; participants made a response to a target stimulus. Therefore, the fCRP in the stimulus-response task solely reflected the behavioural-relevance of the sensory effect.

In both the movement-learning task and the stimulus-response, participants engaged in voluntary movements prior to the occurrence of the sensory effect. However, in the stimulus-response task, participants were informed that their movements did not cause the sensory effect. Thus, the sensory effect was unrelated to the preceding movements. In the movement-learning task, the novelty P3 was contaminated with the fCRP. Unlike the novelty P3, the amplitude of the fCRP did not vary with the learning of a movement heuristic, and was also present in the non-learning tasks in Experiment 1. Collectively, these findings demonstrated that the fCRP is enhanced by the outcome of voluntary movements, and may reflect an initial coupling between movements and sensory outcomes. Thus, the outcomes of voluntary movement may have more behavioural-relevance since they inform future behaviour (Haggard, 2005).

2.6 Conclusion

These findings extend previous studies demonstrating the role of the fCRP in performance monitoring and the role of the P3 in learning. Additionally, the present study highlights an integrative role of the fCRP and the novelty P3 for the acquisition of a movement heuristic. While the fCRP indicates that the desired sensory effect has been attained and its association with the preceding movement, the novelty P3 engages stimulus-driven attentional mechanisms to determine the primary aspects of movement and context required to elicit the sensory effect.
Chapter 3: Altered performance monitoring and enhanced outcome evaluation in medicated individuals with Parkinson’s disease
Chapter 3
Altered performance monitoring and enhanced outcome evaluation in medicated individuals with Parkinson’s disease

3.1 Abstract

Learning the relationship between our movements and their sensory outcomes is dependent on the monitoring and evaluation of these outcomes. This learning process is thought to govern the formation of goal-directed movements. Recently, it has been proposed that patients with Parkinson’s disease (PD) have an increased reliance on a goal-directed mode of movement, due to a loss of dopamine to striatal regions responsible for habitual movements. Additionally, dopamine medication in PD has been proposed to accentuate associations between actions and positive outcomes. Event-related potential (ERP) measures of performance monitoring and outcome evaluation were used to investigate whether there is an altered monitoring and evaluation of outcomes in dopamine-medicated persons with PD compared to healthy age-matched controls. ERPs were recorded during movement-outcome learning and non-learning tasks, and during a stimulus-response task. Individuals with PD had enhanced novelty P3 amplitudes compared to controls in tasks requiring the updating of movement-related information for task performance. Additionally, an enhancement in feedback correct-related positivity (fCRP) amplitude in PD patients was found in the stimulus-response task, indicating altered performance monitoring. These results suggest that in dopamine-medicated persons with PD, unexpected sensory outcomes are monitored and evaluated like unanticipated outcomes of voluntary movement. Both altered performance monitoring and enhanced outcome evaluation may contribute to a heightened sense of control in dopamine-medicated PD.
3.2 Introduction

The outcome of our actions greatly affects future behaviour (cf. Thorndike, 1911). By monitoring and evaluating these outcomes the brain can create movement heuristics or efficient rules to guide behavioural selection (Chapter 2). Dopamine and the basal ganglia have a unique role in the plasticity of these movement heuristics. Striatal dopamine has been proposed to mediate future behavioural selection (Redgrave and Gurney, 2006; Redgrave et al., 2008) by modifying the efficacy of corticostriatal synapses (Reynolds et al., 2001). Disruption of adaptive behavioural selection and expression are observed when there is dysfunction of normal dopaminergic activity in the brain (e.g. in Parkinson’s disease).

In Parkinson’s disease (PD), the progressive loss of dopamine activity in the striatum results in symptoms that are predominately movement-related (e.g. tremor, rigidity, slowness of movement, and impeded gait). Underlying these movement-related impairments is the loss of dopamine innervation to the sensorimotor territories of the striatum, the dorsal and posterior regions (Bernheimer et al., 1973; Frey et al., 1996; Kish et al., 1988). Reduced dopaminergic activity in the sensorimotor striatum causes an abnormal increase in the inhibitory signalling from the basal ganglia output nuclei (DeLong and Wichmann, 2007; Obeso et al., 2008). Increased inhibitory signals to the motor cortex (via the thalamus) reduce plasticity in the motor cortex (Morgante et al., 2006). This loss of plasticity may be responsible for the disruption of well-learned or automatic movements such as facial expressions, blinking, speech, and gait (Marsden, 1982).

Because the loss of dopamine innervation in the early phases of PD is predominately in the sensorimotor territories, and many of the movement-related symptoms are disruptions of well-learned behaviours, a recent review has proposed that there is a diminution of the habitual mode and an increased reliance on a goal-directed mode of movement (Redgrave et al., 2010). Indeed, studies in both animals and humans have demonstrated that the sensorimotor corticostriatal loop mediates the habitual mode of movement, while the associative corticostriatal loop mediates the goal-directed mode (for a review see Balleine and O'Doherty, 2009). In the goal-directed mode, movements are dependent on their outcomes. As a result, an increase in cognitive effort is required to monitor performance (Redgrave et al., 2010; Schneider and Chein, 2003). Thus, both
the loss of normal habits and the continual reliance on cognitive effort to monitor movements may result in a debilitating load on attentional processes in PD. Indeed, patients with PD have difficulties with dual-task performance (e.g. Benecke et al., 1986; Brown and Marsden, 1991; Canning, 2005; Schwab et al., 1954), slowed task-set switching (e.g. Shook et al., 2005; Woodward et al., 2002), and executive dysfunction (e.g. Brown and Marsden, 1990; Dubois and Pillon, 1996; Rodriguez-Oroz et al., 2009).

Levodopa (L-Dopa) medication is commonly used to restore movement-related function in PD. L-Dopa therapy ameliorates movement-related symptoms of PD by elevating striatal dopamine levels (Hornykiewicz, 1974; Maruyama et al., 1996), thereby restoring dopamine levels in sensorimotor territories of the striatum. However, elevated dopamine levels may ‘overdose’ corticostriatal loops and mesocortical dopamine projections that are still relatively intact in PD (Gotham et al., 1988). This dopamine-overdose hypothesis has been supported by numerous studies (e.g. Cools et al., 2001; Frank et al., 2004; Moustafa et al., 2008; Swainson et al., 2000).

With the goal-directed mode of movement intact in PD, dopamine medication may alter the monitoring and evaluation of movement-related outcomes. Individuals with PD ON dopamine medication have been shown to have an enhanced sensitivity to positive stimuli (Frank et al., 2004) and increased learning rates for positive outcomes (Rutledge et al., 2009). Additionally, dopamine medication can induce pathological gambling in PD (Avanzi et al., 2006; Dodd et al., 2005; Molina et al., 2000). It has been proposed that dopamine medication boosts the association between betting behaviour and winning outcomes, but weakens the association with losing outcomes (Pessiglione et al., 2006; Voon et al., 2010), thereby creating an erroneous sense of control over the outcomes. This notion is supported by enhanced action-effect binding when patients with PD were ON dopamine medication (Moore et al., 2010b).

A heightened sense of control, induced by dopamine medication, may stem from altered monitoring and evaluation of outcomes that follow behavioural action. It has been proposed that dopamine medication may ‘overdose’ intact striatal regions by altering striatal plasticity (Cools, 2006). This amplified plasticity may mediate the proposed dopamine medication enhancement of the updating signal the basal ganglia sends to the cortex (O’Reilly and Frank, 2006). Indeed, Moustafa, Sherman, and Frank
(2008) found that patients ON dopamine medication had difficulties ignoring distracting stimuli during a working memory task, suggesting that an enhanced basal ganglia updating signal altered stimulus monitoring and evaluation.

The monitoring and evaluation of movement-related outcomes has been proposed to occur within the basal ganglia (Holroyd and Coles, 2002; Holroyd and Coles, 2008) and anterior cingulate cortex (ACC; e.g. Behrens et al., 2007; Holroyd and Coles, 2002; Holroyd and Coles, 2008; Rushworth et al., 2007a). Walton, Delvin, and Rushworth (2004) found that activity in the ACC was highest when movements were freely chosen and participants had to monitor the outcome of their movements. By monitoring and evaluating the outcomes of voluntary movements, the ACC is proposed to guide behavioural selection by creating a reinforcement history (i.e. collection of previous outcomes) for previous movements (Holroyd and Coles, 2008; Rushworth et al., 2007a). Additionally, activity within the mesocortical dopamine system principally targets the ACC (Paus, 2001).

Source generation analysis indicates that the feedback error-related negativity (fERN) and the P3, both event-related potential (ERP) measures of outcome monitoring and evaluation, are generated by activity in the ACC (Zhou et al., 2010). Findings from Chapter 2 demonstrate an integrative role of the feedback correct-related positivity (fCRP) and the novelty P3 in monitoring and evaluating outcomes to create a movement heuristic. The fCRP, the influential subcomponent of the fERN, indicated the attainment of a desired outcome by the selected voluntary movements. Additionally, the novelty P3, which is a specific instance of the ubiquitous P3, reflects the engagement of stimulus-driven attentional mechanisms to evaluate the outcome, as well as any recently performed voluntary movements. Therein, the novelty P3 initiates the process of determining the primary aspects of movement and context that were responsible for the occurrence of the desired outcome. Previous studies have shown alterations in the outcome-related ERPs in non-medicated individuals with PD compared to controls (Falkenstein et al., 2001; Poceta et al., 2006; Wang et al., 1998).

The aim of the present study was to investigate the whether the proposed heightened sense of control in dopamine-medicated persons with PD is the result of altered monitoring and evaluation of outcomes that follow behavioural action. Specifically, behavioural performance, and fCRP and novelty P3 ERPs measures were
recorded during movement-outcome learning and non-learning tasks, and during a stimulus-response task. Behavioural performance and ERPs from individuals with PD ON dopamine medication were compared to healthy age-matched controls. It is important to note that in all the tasks only positive feedback was used because dopamine medication in PD differentially affects sensitivity to positive and negative feedback (Frank et al., 2004).

Based on the notion that there is a heightened sense of control in medicated persons with PD, it was hypothesized that the amplitude of fCRP amplitude should be larger compared to the control group. It was also hypothesized that the novelty P3 amplitude in the PD group will be enhanced in comparison to the control group, based on the idea that dopamine medication amplifies the updating signal from the basal ganglia.

3.3 Methods

3.3.1 Participants

Eight patients with mild to moderate PD were recruited from the Otago Parkinson’s Society, Dunedin, NZ (see Table 3.1 for patient details). Inclusion criteria were: no known dementia (Mini-Mental State Exam score $\geq 27$), no current depressive symptoms (Geriatric Depression Scale score $\leq 5$), and currently on dopamine medication.

Eight age- and sex-matched healthy controls were recruited from a University of Otago database of older adults participants (Table 3.1). Inclusion criteria were: no known neurological or psychiatric illnesses, no known dementia (MMSE score $\geq 27$), and no current depressive symptoms (GDS score $\leq 5$). The Lower South Otago Regional Ethics Committee approved all procedures. All participants volunteered and gave their fully informed consent.
Table 3.1 Demographic, pathology, and drug details in PD patients and controls.

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3.3.2 Stimuli

The stimuli used in this study were similar to the stimuli described in Chapter 2 (sections 2.3.1 and 2.4.1). However, the sizes of stimuli were adjusted for use with an older population. The visual angle of the green circle sensory outcome was 4.04°, the central grey fixation cross was 0.8°, the grey circle used as the cursor was 0.8°, and the grey outline of a circle in the two non-learning tasks and the ‘hot spot’ in the movement-learning task were 4.04°.

3.3.3 Experimental procedure

Prior to the experimental session, patients and controls were interviewed. During the interview current medical history was obtained, including current PD treatment medication for patients. Neuropsychological tests were also administered to screen for dementia and depression. The motor portion of the UPDRS was administered to patients.

The movement-learning task, the continuous-cue and initial-cue non-learning movement tasks (Figure 2.1A-C), and the stimulus-response task (Figure 2.4B) were performed in a similar manner as described in Chapter 2 (sections 2.3.1 and 2.4.1). However, all tasks were performed in a single experiment with three blocks of each task. In total 12 blocks were conducted, with a block of the continuous-cue task and a block of the initial-cue task following each block of the movement-learning task in a counterbalanced design (i.e. ABC-ABC-ABC or ACB-ACB-ACB). Three blocks of the stimulus-response task followed these nine blocks.

3.3.4 EEG data acquisition

Electroencephalography (EEG) and electrooculography (EOG) data were collected following the protocol and setup described in Chapter 2 (section 2.3.1).

3.4 Data analysis

3.4.1 Behavioural analysis

The hit rate was used as a behavioural measure of performance in the movement-learning task and the two non-learning task as described in Chapter 2 (section 2.3.2). For the stimulus-response task, the time it took the participants to
respond to each green circle by moving to the fixation cross, and the number of responses made were recorded. The mean response time and the mean number of responses were computed for the first half of green circle occurrences (1–15; F15) and second half of green circle occurrences (16–30; L15) of each block.

### 3.4.2 EEG analysis

Continuous EEG data were epoched and baseline corrected relative to the 200 msec period prior to stimulus onset in a similar manner as described in Chapter 2 (section 2.3.2). However, prior to averaging, epochs containing ocular artefacts were corrected (Gratton et al., 1983). Additionally, to remove movement artefacts associated with PD, EEG data were then wavelet decomposed to level 9 using a ‘Daubechies 6’ discrete wavelet transformation, and reconstructed with 1-25Hz-frequency range. Based on visual inspection of the averaged waveform, the mean amplitude of the fCRP was measured at the Cz electrode site and averaged across the time window 210–290 msec, and the novelty P3 was measured at the Cz electrode site and averaged across the time window 300–550 msec.

### 3.4.3 Statistical analysis

The measured variables were entered into separated mixed ANOVAs with the within-subjects factors of task (movement-outcome learning, continuous-cue, initial-cue, stimulus-response), block-half (F15, L15) and block (Block 1, Block 2, Block 3), and between-subject factor of group (patients, controls). To tease apart specific effects of interactions, additional repeated-measures ANOVAs and planned comparisons were used where appropriate to test our hypotheses. Effects were considered significant if p < .05. Greenhouse–Geisser corrections were also applied to p-values where appropriate. Effect sizes are shown using partial eta squared ($\eta^2$). All statistical tests were conducted using SPSS (version 18.0) software.

### 3.5 Results

#### 3.5.1 Behavioural results

There were no significant differences between patients with PD and healthy controls in hit rate for the movement-learning task. The only significant main effect of group was found in the continuous-cue task, F(1,14) = 4.18, p = .046, $\eta^2 = .28$. The hit
rate for the PD group (M = 1.45, SE = .13) was significantly smaller than the control group (M = 1.84, SE = .13). Also, no significant differences between groups in mean response time and number of responses were found for the stimulus-response task (Figure 3.1).

In general, separate ANOVAs for the PD group and the control group demonstrated learning-related changes in hit rate. In the PD group, a significant main effect of block-half was found in the movement-learning task, $F(1,7) = 23.71, p = .002, \eta^2 = .77$, with the hit rate significantly lower in the first block-half ($M = .61, SE = .10$) compared to the second block-half ($M = .95, SE = .13$). For the control group there was a significant main effect of both block-half, $F(1,7) = 99.30, p < .001, \eta^2 = .93$, and block, $F(2,14) = 7.51, p = .008, \eta^2 = .52$. The hit rate in the first block-half ($M = .68, SE = .11$) was significantly lower than the hit rate in the second block-half ($M = 1.2, SE = .13$).
3.5.2 Novelty P3 results

Average ERP waveforms for the AMC and PD groups are presented in Figure 3.2. The mixed measures ANOVAs demonstrated a significant main effects of group, F(1,14) = 7.69, p = .015, η² = .36, with a larger novelty P3 in the PD group (M = 8.46 μV, SE = .74 μV) compared to the AMC group (M = 5.56 μV, SE = .74 μV). This enhancement of novelty P3 amplitude in the PD group compared to the control group was present in the movement-learning task, F(1, 14) = 5.95, p = .029, η² = .30 (Figure 3.2A), the initial-cue task, F(1, 14) = 5.56, p = .033, η² = .28 (Figure 3.2C), and the stimulus-response task, F(1, 14) = 4.60, p = .05, η² = .25 (Figure 3.2C).

Separate ANOVAs for the PD group and the AMC group were conducted to separately look at task related changes. For the PD group there was a significant main effect of task, F(3,21) = 9.64, p = .005, η² = .58. Specific comparisons between tasks demonstrate significant differences between the movement-learning and the continuous-cue task, F(1,7) = 16.88, p = .005, η² = .70, and between the movement-learning and the continuous-cue task, F(1,7) = 9.94, p = .016, η² = .59, with novelty P3
in the movement-learning task (M = 11.53 µV, SE = 1.36 µV) larger than both the continuous-cue task (M = 5.72 µV, SE = .51 µV) and the initial-cue task (M = 6.70 µV, SE = .50 µV). No significant difference between movement-learning and the stimulus-response task was found. Difference waves and the corresponding scalp distributions illustrate the difference across tasks (Figure 3.3).

Similarly, for the AMC group there was a significant main effect of task F(3,21) = 11.51, p = .005, η² = .62. Specific comparisons between tasks demonstrate significant differences between the movement-learning and the continuous-cue task F(1,7) = 46.90, p < .001, η² = .87, and between the movement-learning and the continuous-cue task, F(1,7) = 27.63, p = .001, η² = .80, with novelty P3 in the movement-learning task (M = 7.40 µV, SE = 1.01 µV) larger than both the continuous-cue task (M = 4.01 µV, SE = .85 µV) and the initial-cue task (M = 4.37 µV, SE = .85 µV). No significant difference between movement-learning and the stimulus-response task was found. Difference waves and the corresponding scalp distributions illustrate the difference across tasks (Figure 3.4).

Similar to hit rate, separate ANOVAs for the PD group and the AMC group demonstrated learning-related changes in novelty P3 amplitude in the movement-learning task. For the PD group there was a main effect of block-half, [F(1,7) = 12.50, p = .01, η² = .64], with novelty P3 amplitude in the first block-half (M = 12.61 µV, SE = 1.45 µV) larger than novelty P3 amplitude in the second block-half (M = 10.45 µV, SE = 1.33 µV). Also, in the AMC group there was a significant main effect of block-half, [F(1,7) = 10.68, p = .014, η² = .60], with novelty P3 amplitude in the first block-half (M = 8.66 µV, SE = 1.20 µV) was significantly larger than novelty P3 amplitude in the second block-half (M = 6.13 µV, SE = .94 µV).

For the stimulus-response task, there was a significant main effect of block-half only in the AMC group, F(1,7) = 93.30, p < .001, η² = .93, with novelty P3 amplitude of the first block-half (M = 6.49 µV, SE = .87 µV) significantly larger than the second block-half (M = 4.17 µV, SE = .87 µV). Additionally, in the AMC group there was a significant main effect of block-half in the initial-cue task, F(1,7) = 12.41, p = .010, η² = .64, with a significantly larger novelty P3 amplitude found in the first block-half (M = 4.51 µV, SE = .82 µV) compared to the second block-half (M = 2.88 µV, SE = .59 µV). For the PD group in the continuous-cue task there was a significant main effect of
block, F(2,14) = 11.49, p = .002, η² = .62. Pairwise comparisons indicated that the first block (M = 6.81 μV, SE = .48 μV) was significantly larger than the second block (M = 3.90 μV, SE = .72 μV), p = .012, and the third block (M = 3.66 μV, SE = .76 μV), p = .006.

Figure 3.3 (A) Average ERP difference waveforms from age-match controls at Cz electrode site for movement-learning task – continuous cue task (purple line), movement-learning task – initial cue task (blue line), and movement-learning task – stimulus-response task (orange line). Scalp distributions for the time point where the difference waves reach peak amplitude for movement-learning task – continuous cue task (B), movement-learning task – initial cue task (C), and movement-learning task – stimulus-response task (D). (B) and (C) difference wave scalp distributions show a central distribution, consistent with observed scalp distributions for the novelty P3. Blue and red coloring represents negative and positive intensity on the scalp distribution, respectively.
Figure 3.4 (A) Average ERP difference waveforms from PD participants at Cz electrode site for movement-learning task – continuous cue task (purple line), movement-learning task – initial cue task (blue line), and movement-learning task – stimulus-response task (orange line). Scalp distributions at the time point where the difference waves reach peak amplitude for movement-learning task – continuous cue task (B), movement-learning task – initial cue task (C), and movement-learning task – stimulus-response task (D). (B) and (C) difference wave scalp distributions show a central distribution, consistent with observed scalp distributions for the novelty P3. Blue and red coloring represents negative and positive intensity on the scalp distribution, respectively.

3.5.3 fCRP results

The only significant differences in performance monitoring, as measured by fCRP amplitude, occurred in the stimulus-response task when comparing the PD group (M = 6.53 μV, SE = .80 μV) and the control group (M = 3.28 μV, SE = .80 μV), F(1, 14) = 8.40, p = .012, η² = .36 (Figure 3.3). Also, only in the control group was there a significant difference in fCRP amplitude between the movement-learning task (M = 5.14 μV, SE = .60 μV) and the stimulus-response task (M = 3.28 μV, SE = .60 μV). This difference in the fCRP between the movement-learning task and the stimulus-response task is demonstrated by the computed difference wave (Figure 3.4A) and the
associated scalp distribution (Figure 3.4D). Additionally, the lack of difference between the movement-learning task and the stimulus-response task for the PD group is highlighted by the difference wave (Figure 3.5A) and scalp distribution (Figure 3.5D).

3.6 Discussion

This study provides an initial investigation into how the proposed heightened sense of control in dopamine-medicated persons with PD might affect ERPs associated with outcome evaluation. ERP results support the notion that dopamine medication in PD leads to excessive updating signals from the basal ganglia (Moustafa et al., 2008), and suggests altered performance monitoring may lead to an enhanced sense of control (Moore et al., 2010b).

3.6.1 Enhanced updating signal

Individuals with PD ON dopamine medication demonstrated an overall enhancement in novelty P3 amplitude compared to healthy age-matched controls. Enhancement of novelty P3 amplitude in the PD group was most prominent in the movement-learning task. However, there was no difference in behavioural performance between the PD group and the control group for the movement-learning task. The only significant difference in behavioural performance between the two groups was found in the continuous-cue task. Thus, it appears that there was a functional dissociation between novelty P3 amplitude and behavioural performance in the PD group. It may be that dopamine medication restored function of the sensorimotor loop, but overdosed the associative loop (Cools et al., 2001).

The finding of an overall enhancement of novelty P3 amplitude extends previous findings of an enhanced basal ganglia updating signal (Frank et al., 2004; Moustafa et al., 2008) by providing a potential neural correlate. The associative loop is proposed to use feedback-related information to update mental representation by modulating activity in the cortex (Kimura and Graybiel, 1995; Seger, 2008). As a result, the associative loop has been proposed to mediate the learning of the relationship between movements and their outcomes (Balleine and O'Doherty, 2009). Analogous to the associative loop, the novelty P3 is thought to be a measure of cortical activity associated with the updating of mental representations (Friedman et al., 2001). Also, P3 amplitude is correlated with learning (Groen et al., 2007; Jongsma et al., 2006; Lindin...
et al., 2004; Sailer et al., 2010), including the learning of the relationship between movements and their outcome (Chapter 2). Thus, based on the present results, dopamine medication likely enhanced the updating signal from the intact associative loop in persons with PD.

These results also suggest that dopamine medication enhanced normal updating signals, rather than creating erroneous updating signals. Novelty P3 amplitude enhancement only occurred in tasks where updating movement-related mental representations was necessary for task performance. No enhancement in the continuous-cue control task was found in the PD group. Thus, dopamine medication likely enhanced updating signals necessary for evaluating outcomes that informed or update a movement heuristic.

3.6.2 Uncertainty and bottom-up processing may underlie learning-related enhancement of novelty P3 amplitude

No learning related differences were found in novelty P3 amplitude between the movement-learning task and the stimulus-response task for either the PD group or the control group. Previously, novelty P3 amplitude was enhanced in the movement-learning task compared to the stimulus-response task (Chapter 2). However, there were no interspersed blocks of the non-learning movement tasks in that experiment when this comparison was made (Chapter 2, Experiment 2). There were drastic reductions in novelty P3 amplitude from block to block of the movement-learning task in Chapter 2 when there were interspersed blocks of the non-learning movement tasks (Experiment 1). This suggests that participants were learning how to cause the sensory outcome from exposure to the non-learning tasks that employed a similar movement heuristic. With regards to the present study, this refinement of the movement heuristic outside of the movement-learning task may explain the lack of learning-related differences in novelty P3 amplitude between the movement-learning task and the stimulus-response task. The sensory outcome was unexpected rather than providing important information for forming a movement heuristic.

In addition to receiving projections from the basal ganglia via the thalamus, the ACC also has extensive connections with the prefrontal cortex (PFC; Paus, 2001). The PFC has been proposed to be a ‘Goal Processor’ that exerts top-down influence on the
Outcome monitoring and evaluation in PD

ACC (Schneider and Chein, 2003). Additionally, the PFC is involved in working memory processes (Braver et al., 1997). In the non-learning movement tasks, moving the cursor to an observable location on the screen attained the desired outcome. The heuristic for obtaining the desired outcome in the movement-learning task was the same, although the location was not observable. Thus, the ‘location’ movement heuristic may have been maintained within working memory in the PFC. Top-down information from the PFC regarding this movement heuristic may have assisted the ACC in voluntary movement selection, therein, reducing the level of uncertainty in selection. Indeed, the goal of learning is to reduce the uncertainty and improve the efficiency of behavioural selection.

As a result of top-down information providing a viable movement heuristic, the amount of unique information conveyed by the outcome, via bottom-up processing in the basal ganglia, regarding the movement heuristic would be reduced. A previous study conducted by Mars et al. (2008) used trial-by-trial analysis of the P3 to demonstrate that the unique information conveyed by a surprising stimulus determines P3 amplitudes. When none or little top-down information is available, there is a reduction in the certainty that the selected voluntary movement will elicit the desire sensory outcome. As a result, the sensory outcome provided much of the information regarding the movement heuristic.

3.6.2 Altered performance monitoring and the sense of control

In the stimulus-response task an enhancement in fCRP amplitude was observed in the PD group, but not the control group. Previously, it was found that fCRP amplitude was enhanced by the outcome of voluntary movements (Chapter 2), reflecting an increase in performance monitoring. Along these lines, the fCRP has been proposed to indicate the achievement of a task goal (Holroyd et al., 2008). Additionally, fCRP amplitude is enhanced by behaviourally relevant stimuli (Potts et al., 2006; Potts, 2004; Potts et al., 1996). Thus, it appears that goal-directed movements, which are dependent on outcomes, enhance fCRP performance monitoring. Following this proposal, fCRP amplitude in the control group was larger for outcomes caused by voluntary movements compared to when stimuli indicated a response was required. However, in the PD group there was no difference in fCRP amplitude between the movement-learning task and the stimulus-response task.
This lack of difference in fCRP amplitude between the movement-learning task and the stimulus-response task in medicated persons with PD may suggest alterations in performance monitoring. It has been proposed that the outcomes of voluntary movements, because they are intentional, are closely monitored (Haggard, 2005). A recent study has demonstrated that the sense of control over rewarding outcomes can modify performance monitoring and the fCRP (Li et al., 2011). With regard to fCRP findings in the present study, it would appear that altered performance monitoring might have induced a heightened sense of control over sensory events in the stimulus-response task.

As discussed above, learning the relationship between movements and their outcomes, and learning stimulus-response associations, have been proposed to be mediated by the associative and sensorimotor loops, respectively (Balleine and O'Doherty, 2009). It has been demonstrated that ideomotor learning, or movement-outcome learning, is dependent on the voluntary performance of movements (Herwig et al., 2007; Herwig and Waszak, 2009). Additionally, choice (or the voluntary performance of a behaviour) has been shown to modulate outcome-monitoring processes that mediate the fCRP (Peterson et al., 2010; Walton et al., 2004). Thus, outcomes of voluntary movements appear to be monitored in a unique fashion.

In PD, there is a proposed increased reliance on a goal-directed mode of movement (Redgrave et al., 2010). This compulsory dependence on goal-directed control, because of dysfunction of the habitual mode, may result in monitoring of all stimuli in a similar manner as outcomes of voluntary movement, thereby creating a heightened sense of control. Dopamine medication appears to enhance this monitoring bias, rather than ameliorating it by restoring dopamine levels in the sensorimotor striatum.

### 3.6.3 Heightened sense of control

The present study provides clear evidence for a heightened sense of control in dopamine-medicated persons with PD. As demonstrated previously, a heightened sense of control has been proposed to account for the occurrence of pathological gambling in dopamine-medicated patients (Avanzi et al., 2006; Dodd et al., 2005; Molina et al., 2000; Moore et al., 2010b; Pessiglione et al., 2006; Voon et al., 2010). Both enhanced
outcome evaluation and altered performance monitoring contributed to the heightened sense of control.

Additionally, the present study extends the recent finding that dopamine medication in PD patients boosts the association between movements and positive outcomes by modulating activity in the striatum (Pessiglione et al., 2006). Linking movements with outcomes is not solely dependent on the striatum; rather the striatum may provide the ACC with relevant activity necessary for compiling reinforcement histories (Holroyd and Coles, 2008; Rushworth et al., 2007a). Because the ACC has unique connections with the PFC and the basal ganglia, the ACC can use both bottom-up processes and top-down processes to inform voluntary selection (Paus, 2001). The present results indicate that exaggerated bottom-up processing (Cools et al., 2010) mediated by amplified plasticity in the associative striatum creates a bias so that all sensory outcomes are monitored and evaluated like outcomes of voluntary movement. A reduction in the evaluation of negative outcomes may additionally amplify the heightened sense of control by distorting the reinforcement history of behaviours (Voon et al., 2010).

3.7 Conclusion

Using ERP measures, the effect of dopamine medication in the proposed heightened sense of control in individuals with PD was discovered to be a function of enhanced outcome evaluation and altered performance monitoring. Brain activity in dopamine-medicated persons with PD suggested that unexpected sensory outcomes are monitored and evaluated like outcomes of voluntary movement. Additionally, exaggerated bottom-up processing may have contributed to this amplified monitoring and evaluation of outcomes. Behavioural performance was not impaired by this heightened sense of control. Thus, the increased monitoring and evaluation of outcomes may form a compensatory mechanism to bypass the loss of habits.
Chapter 4: Who did it? Event-related potentials of the judgment of agency
Chapter 4
Who did it? Event-related potentials of the judgment of agency

4.1 Abstract

The sense of agency is essential for the experience of control over our movements and their resulting sensory outcomes. Recently, it has been proposed that the sense of agency arises from anticipation and monitoring of the consequences of voluntary movements. Additionally, voluntary movements have been shown to enhance event-related potentials (ERPs) associated with outcome anticipation (the novelty P3) and monitoring (the feedback correct-related positivity; fCRP). In the present experiment these outcome-related ERPs were recorded during a judgment of agency task. In the task, movement-related perceptual cues were manipulated to modulate the degree of sensorimotor congruency and intentional movement-outcome coupling. fCRP amplitude and the proportion of agency judgments were highest when movement-related perceptual cues indicated a high degree of sensorimotor congruency. Additionally, enhanced fCRP amplitude distinguished sensory outcomes preceding agency judgments from sensory outcomes preceding non-agency judgments even when there was low sensorimotor congruency. As a result, the fCRP might be an indicator of monitoring the extent of intentional movement-outcome coupling that underlies the feeling of agency. When fCRP amplitudes were similar for sensory outcomes preceding agency and non-agency judgments, the novelty P3 was the differentiating factor for the judgment of agency. Thus, this suggests that the novelty P3 gauges discrepancies in anticipation across multiple authorship cues. Finally, the cognitive state at the time of the sensory outcome may have affected the subsequent processing of the movement-outcome information necessary for the judgment of agency.
4.2 Introduction

In our everyday lives we have the experience of being in control of our movements and the sensory outcomes they elicit. This sense of agency allows us to distinguish between outcomes caused by our own actions from outcomes produced by others. Our sense of control over sensory outcomes (elicited by voluntary movements) originates from learning mechanisms that associate voluntary movements and sensory outcomes that often occur together (Hommel and Elsner, 2009).

In this vein, the ideomotor theory states that voluntary movements are selected in relation to their anticipated sensory outcomes (Elsner and Hommel, 2001). Previous studies have demonstrated that the linking of voluntary movements with sensory outcomes occurs through ideomotor learning (e.g. Elsner et al., 2002). Additionally, ideomotor learning only occurs when the movement has been initiated in a voluntary or intentional mode (Herwig et al., 2007; Herwig and Waszak, 2009). As a result, learning establishes the predictive link between intentional movements and sensory outcomes that gives rise to the sense of agency (Haggard and Tsakiris, 2009; Spengler et al., 2009).

When investigating the sense of agency, it is important to consider distinctions between the two levels of agency: the feeling of agency and the judgment of agency (David et al., 2008; Synofzik et al., 2008a, b). The feeling of agency is a pre-reflective and implicit experience that is heavily linked to the intentional initiation of movement (Haggard and Tsakiris, 2009; Synofzik et al., 2008a, b). In addition, intentionally initiating voluntary movement changes our perception of sensory outcomes (Herwig and Waszak, 2009). Haggard, Clark and Kalogeris (2002) found that the performance of intentional movements induced an attraction between the perceived time of a movement and the sensory outcome. This intentional binding effect has been proposed to reflect subjective feelings of agency (Haggard et al., 2002). Synofzik, Vosgerau, and Newen (2008a, b) have suggested that the feeling of agency is the result of a weighting process of movement-related perceptual (e.g. visual feedback) and motor cues (e.g. efference copies). Moreover, in tasks where there is an explicit goal, “the coupling between motor intentions and the goal might become largely important for the [feeling of agency]” (Synofzik et al., 2008a, p. 227).
The judgment of agency is the reflective and explicit attribution of agency (Synofzik et al., 2008a, b). Normally, the feeling of agency is necessary for the judgment of agency (Haggard and Tsakiris, 2009). Thus, a degree of coupling between motor intentions and the goal is required for the judgment of agency. However, the feeling of agency is not sufficient for the judgment of agency (Haggard and Tsakiris, 2009). The judgment of agency requires the evaluation of movement-outcome information (Haggard and Tsakiris, 2009).

As previously shown, the feedback correct-related positivity (fCRP) event-related potential (ERP) was enhanced by sensory events that were caused by voluntary movements (in both learning and non-learning tasks) compared to sensory events requiring a response movement (Chapter 2). Additionally, the performance of a movement has been shown to enhance the feedback error-related negativity (fERN) to sensory outcomes (Zhou et al., 2010). The fCRP is the influential positive subcomponent of the fERN (Holroyd et al., 2008). The basic role of the fERN/fCRP in outcome monitoring is to indicate whether or not the task goal has been achieved (Hajcak et al., 2006; Holroyd et al., 2006; Holroyd et al., 2008), with the fCRP specifically indicating that the task goal has been achieved. Thus, the fCRP may index the movement-goal coupling needed for the feeling of agency.

Given that the feeling of agency is normally necessary for the judgment of agency, the aim of the present study was to investigate the role of the fCRP in judgments of agency. Previous findings suggest that the novelty P3 engages attentional processes necessary for the evaluation of movement-outcome information (Chapter 2; Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007). Thus, the effect of the novelty P3 on judgments of agency was also investigated. Additionally, presence of the novelty P3 indicated that the sensory outcome was unanticipated (Chapter 2; Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007). Therefore, it was hypothesised that agency judgments would be associated with increased fCRP amplitude and decreased novelty P3 amplitude compared with judgments of non-agency. Movement-related perceptual cues were manipulated in the judgment of agency task employed, in order to modulate the degree of movement-goal coupling.
4.3 Methods

4.3.1 Participants

The participants were 12 students (10 males), aged 19-39 years (mean age 24 years) from the University of Otago. All participants were part of a voluntary participant pool in the Department of Psychology at the University of Otago (Dunedin, New Zealand). Prior to the experiment, participants were given an information sheet and informed consent was obtained. The Lower South Otago Regional Ethics Committee approved all procedures.

4.3.2 Stimuli

The sensory outcome was a green circle (2.02 ° visual angle) presented for 100 msec within the grey outline of a circle (2.02°) that participants were instructed to move the cursor into. The cursor was a grey circle (0.4°) controlled by a tracking-ball mouse. In 25% of the trials, the specific location (hot spot) on the screen (that would elicit the sensory outcome when the cursor was moved into it) was defined by the grey outline of a circle visible to the participants (Figure 4.1A). In another 50% of the trials, the hot spot was an invisible circle that was slightly wider (2.82°) than the visible grey outlined circle (Figure 4.1B). In the remaining 25% of trials, the hot spot was an invisible circle that was much wider (4.82°) than the visible grey outlined circle (Figure 4.1C).

Prior to the start of each trial, the text stimulus ‘READY’ (3.45°) was presented for 500 msec followed by a central grey fixation cross (0.4°) for 250 msec. The visible grey outlined circle would then be presented in a random location on the screen, and the cursor was presented central over the fixation cross. The participant would then perform the required action (see “Experimental procedure”). Following each trial (500 msec following the sensory outcome) the text stimulus (3.45°), ‘Did you cause the green stimulus? (Y/N)’ would appear on the screen. The text was removed following a response of the ‘N’ or ‘Y’ key on the keyboard. A blank screen was presented for 500 msec following the response. All visual stimuli were presented against a black background on a 54cm display. MatLab software (MathWorks, Inc., vR2008a) was used for all stimulus presentation and collection of behavioural responses.
4.3.3 Experimental procedure

Participants were informed that they were playing a game against another participant (a confederate was used to make this manipulation believable). The goal on each trial was to move the cursor into a grey outlined circle on the screen to elicit a green circle (within the outlined circle). Participants were further instructed that the green circle would appear on the screen if either their cursor or the other participant’s invisible cursor reached the grey outlined circle. Following each presentation of the green circle they were instructed to judge whether they elicited the green circle or not. Judgments of agency were made by answering ‘yes’ or ‘no’ (pressing Y or N keys on the keyboard, respectively) to the question on the screen ‘Did you cause the green stimulus? (Y/N)’.

In 25% of trials perceptual information clearly indicated to the participants that their cursor movements elicited the green circle, thus providing congruent sensorimotor information with the sense of agency (Figure 4.1A). Conversely, in another 50% of trials, the perceptual information provided could be judged by participants either to indicate that their cursor movements elicited the green circle or that the green circle was not caused by their cursor movements (Figure 4.1B). As a result, sensorimotor information was moderately-incongruent. In the remaining 25% of trials, perceptual information plainly indicated the occurrence of the green circle was not the result of the participants’ cursor movements, and thus potentially provided highly incongruent sensorimotor information regarding agency (Figure 4.1C). There were a total of 60 trials per block, across 4 blocks. The hot spot location varied from trial to trial.
Figure 4.1 Schematic illustration of the three trial-types of the judgment of agency task. In the Congruent trial-type the sensory event occurs when the cursor is within the pre-defined location (A). In the Moderately-Incongruent trial-type the sensory event occurs when the cursor is just outside the pre-defined location (B). In the Incongruent trial-type the sensory event occurs when the cursor is a distance away from the pre-defined location (C). All trials began with ‘Ready’ and ended with the question ‘Did you cause the green stimulus (Y/N)?’.
## 4.3.4 EEG recording and analysis

Electroencephalography (EEG) and electrooculography (EOG) data were collected following the protocol and setup described in Chapter 2 (section 2.3.1). EEG analysis was the same as in Chapter 2 (section 2.3.1). However, based on visual inspection of the averaged waveform, the mean amplitude of the fCRP was measured at the FCz electrode site and averaged across the time window 200–250 msec, and the novelty P3 was measured at the FCz electrode site and averaged across the time window 300–400 msec. Scalp distributions of the 225 msec midpoint fCRP time-window and the 350 msec midpoint of the novelty P3 time window demonstrate the separable distributions for the two components (Figure 4.2).

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**Figure 4.2** Scalp distributions of event-related brain potential (ERP) data recorded at channel Cz averaged according to whether the sensory outcome was preceded an Agency or Non-agency judgment for each of the three trial-types (Congruent, Moderately-incongruent, and Incongruent). 225 msec represents the midpoint fCRP time-window and 350 msec represents the midpoint of the novelty P3 time-window. Note that the fCRP scalp distribution has a fronto-central distribution, while the novelty P3 is more centrally distributed. Blue and red coloring represents negative and positive intensity, respectively.
4.3.5 Statistical analysis

In order to analyse participants’ judgments of agency, the proportion of ‘yes’ and ‘no’ responses for each trial-type were computed. An arc sine square root transformation was performed on the proportional data before entering into a repeated-measures ANOVA with the within-subjects factors Agency (‘yes’, ‘no’) and Trial-type (congruent, moderately incongruent, incongruent). This was followed by separate pairwise comparisons for ‘yes’ and ‘no’ responses with the within-subject factor of Trial-type (congruent, moderately incongruent, incongruent) to look at any differences in responding among trial-types. Additionally, paired-sample t-tests for each trial-type were conducted to specifically examine differences in agency judgments.

Mean amplitude measures of the fCRP and the novelty P3, and novelty P3-fCRP difference amplitudes (computed by subtracting fCRP amplitudes from novelty P3 amplitudes) measured at the FCz electrode site were entered into similar analyses. Effects were considered significant if $p < .05$. Greenhouse–Geisser corrections were applied to p-values where appropriate. Effect sizes are shown using partial eta squared ($\eta^2$). All statistical tests were conducted using SPSS (version 18.0) software.
4.4 Results

4.4.1 Judgments of agency

To analyze participants’ judgments of agency, the arcsine square root transformation of the proportion of ‘yes’ and ‘no’ responses for each trial-type was entered into a repeated-measures ANOVA with the within-subjects factors Agency (‘yes’, ‘no’) and Trial-type (congruent, moderately incongruent, incongruent). A significant main effect of Agency [F(1, 11) = 6.64, p = .026, \( \eta^2 = .37 \)] demonstrated that participants made a significantly greater proportion of Agency judgments (M = .91, SE = .05) than Non-agency judgments (M = .68, SE = .05). Additionally, there was a significant interaction of Agency X Trial-type, F(2, 22) = 40.70, p < .001, \( \eta^2 = .79 \).

To tease apart the above interaction, separate repeated-measure ANOVAs for Agency judgments and Non-agency judgments with Trial-type as the within-subject factor were conducted. A significant main effect of Trial-type was found for both Agency judgments, F(2, 22) = 40.15, p < .001, \( \eta^2 = .79 \), and Non-agency judgments,
F(2,22) = 39.98, p < .001, η² = .79. Pairwise comparisons indicated that there were a significantly higher proportion of Agency judgments for the congruent trial-type (M = 1.14, SE = .04) than for the moderately-incongruent (M = .81, SE = .06, p < .001) and incongruent (M = .77, SE = .06 p < .001) trial-types (Figure 4.3). Conversely, there was a significantly smaller proportion of Non-agency judgments for the congruent trial-type (M = .43, SE = .04) than for moderately-incongruent (M = .76, SE = .06), p < .001, and incongruent (M = .78, SE = .06), p < .001 trial-types.

Paired-sample t-tests for each trial-type, conducted to specifically examine differences in agency judgments within a trial-type, revealed a significant difference between Agency (M = 1.14, SE = .03) and Non-agency judgments (M = .43, SE = .04) only for the congruent trial-type, t(11) = 8.48, p < .001 (Figure 4.3).
Figure 4.4 Event-related brain potential (ERP) data recorded at channel Cz averaged according to whether the sensory outcome was preceded an Agency or Non-agency judgment for each of the three trial-types. (a) Congruent. (b) Moderately-incongruent. (c) Incongruent. Negative is plotted upward by convention. Shaded areas indicate periods during which the fCRP and the novelty P3 were evaluated, respectively.

4.4.2 ERP results

Figure 4.4 presents the ERPs elicited sensory outcome for congruent, moderately-incongruent, and congruent trial-types, separated according to whether the sensory outcome was subsequently followed by an Agency or Non-agency judgment. To determine whether an interaction between the fCRP and novelty P3 was predictive of participants’ judgments of agency, mean amplitude measures of the fCRP and the novelty P3 were entered into a repeated-measures ANOVA with the within-subjects factors Agency (‘yes’, ‘no’), Trial-type (congruent, moderately incongruent, incongruent), and Components (fCRP, P3) as factors. As predicted there were
significant interactions between Component X Agency, $F(1,11) = 8.56$, $p = .014$, $\eta^2 = .44$, and Component X Trial-type, $F(2,22) = 7.44$, $p = .01$, $\eta^2 = .40$ (Figure 4.5A-B).

Separate repeated-measures ANOVAs with the within-subjects factors Agency (‘yes’, ‘no’) and Trial-type (congruent, moderately incongruent, incongruent) conducted for each ERP component revealed there was a significant main effect of Agency for the fCRP, $F(1,11) = 12.62$, $p = .005$, $\eta^2 = .53$, but not for the novelty P3. Agency judgments were preceded by a larger fCRP ($M = 13.13 \mu V$, $SE = 1.52 \mu V$) compared to the fCRP preceding Non-agency judgments ($M = 11.05 \mu V$, $SE = 1.51 \mu V$). There was a significant main effect of Trial-type for both the fCRP, $F(2,22) = 5.73$, $p = .017$, $\eta^2 = .34$, and the novelty P3, $F(2,22) = 4.95$, $p = .019$, $\eta^2 = .31$. Pairwise comparisons for Trial-type indicated that the fCRP elicited by the congruent trial-type ($M = 14.66 \mu V$, $SE = 1.49 \mu V$) was significantly larger than for the moderately-incongruent trial-type ($M = 11.65 \mu V$, $SE = 1.30 \mu V$, $p = .024$).

To further unravel the significant interactions of Component X Agency and Component X Trial-type, a P3-fCRP difference amplitude was computed. A repeated-measures ANOVA with Agency and Trial-type as within-subject factors demonstrated a significant main effect of Agency, $F(1,11) = 8.56$, $p = .014$, $\eta^2 = .44$, indicating that the novelty P3-fCRP difference amplitude for Agency judgments ($M = -1.23 \mu V$, $SE = .93 \mu V$) was significantly smaller than for Non-agency judgments ($M = 1.69 \mu V$, $SE = 1.49 \mu V$, $p = .014$). Additionally, there was a significant main-effect of Trial-type, $F(2,22) = 7.44$, $p = .01$, $\eta^2 = .40$.

Paired-sample t-tests, conducted to examine differences in agency judgments within each trial-type, revealed that the novelty P3-fCRP difference amplitude for Agency judgments in the moderately-incongruent trial-type ($M = -1.34 \mu V$, $SE = .90 \mu V$) was significantly smaller than for Non-agency judgments ($M = 3.87 \mu V$, $SE = 1.25 \mu V$), $t(11) = 6.01$, $p < .001$ (Figure 4.5c). Additionally, the novelty P3-fCRP difference amplitude for Agency judgments in the incongruent trial-type ($M = 1.02 \mu V$, $SE = .66 \mu V$) was significantly smaller than for Non-agency judgments ($M = 4.18 \mu V$, $SE = 1.48 \mu V$), $t(11) = 2.62$, $p = .035$ (Figure 4.5c).
4.5 Discussion

The aim of the present study was to provide an electrophysiological understanding of how monitoring and anticipation of the sensory outcomes of voluntary movements relates to the sense of agency. The difference in amplitude between the fCRP and the novelty P3 seems to be a predictive indicator of the judgment of agency. Collectively, the results support multilevel models of the sense of agency (Synofzik et al., 2008a; Wegner and Sparrow, 2004).
4.5.1 *The fCRP: Monitoring and the feeling of agency*

ERP results showed, overall, that agency judgments were preceded by sensory outcomes with an enhanced fCRP compared to sensory outcomes that were subsequently attributed to another agent. The implicit feel of agency is proposed to contribute to the explicit judgment of agency (Haggard and Tsakiris, 2009; Synofzik et al., 2008a, b). By initially coupling sensory outcomes with intentional movements, the feeling of agency influences the judgment of agency (Synofzik et al., 2008a, b). Based on previous studies it was hypothesized that the fCRP is a potential index of this coupling.

There was a significantly higher proportion of agency judgments for the congruent trial-type compared to both the moderately-incongruent and incongruent trial-types. Thus, when movement-related perceptual cues indicated a high degree of congruency between visual feedback and internal predictions, participants were more likely to make agency judgments. Indeed, an internal comparator of visual feedback with internal predictions has been proposed to play a significant role in the weighting process that results in the feeling of agency (Synofzik et al., 2008b). When there is congruency between visual feedback and internal predictions there is a coherent feeling of control over movements and their sensory effects (Synofzik et al., 2008b).

Originally, the internal comparator was proposed by computational models of motor control with the output of the comparator thought to dictate the sense of agency (e.g. (Berti et al., 2005; Blakemore et al., 2002). However, Synofzik, Vosgerau, and Newen (2008a) pointed out that the match between predicted and actual sensory feedback, as proposed by computational models, cannot account for all instances of the sense of agency.

Importantly, in the present study there was no significant difference in fCRP amplitude for sensory outcomes that led to agency judgments across the different trial-types. This is despite differences in movement-related perceptual cues across the different trial-types. Additionally, fCRP amplitude was only predictive of agency judgments in the incongruent trial-type. As such, these findings support the proposal that in addition to congruency between visual feedback and internal predictions, the coupling between intentional movement and sensory outcomes can be critical for the feeling of agency, particularly in tasks with explicit goals (Synofzik et al., 2008a).
Indeed, the performance of intentional movements alters the perception of time between the movement and the sensory outcome (Haggard et al., 2002). This ‘intentional binding’ effect may be able to override incongruence output from an internal comparator, thereby helping to maintain the feeling of agency.

The present results clearly highlight an association between the feeling of agency and the fCRP, in that the amplitude of the fCRP appears to be modulated by authorship cues that give rise to the feeling of agency. Supporting this link between the fCRP and the feeling of agency, a recent study has demonstrated that the sense of control over rewarding outcomes, similar to the feeling of agency, can modify performance monitoring and the fCRP (Li et al., 2011). When participants were informed that they had “control” over rewarding outcomes, the fCRP was more positive than “uncontrollable” rewarding outcomes. Additionally, Bellebaum, Kobza, Thiele, and Daum (2010) demonstrated that outcome monitoring was enhanced during active learning versus observational learning, further suggesting a link between the fCRP and agency. Indeed, in the present study fCRP amplitude was modulated by congruency between visual feedback and internal predictions, and intentional movement-outcome coupling. However, fCRP amplitude was not the predictive indicator of the agency judgments in all instances. In the moderately-incongruent trials, there was no significant difference in fCRP amplitude between agency and non-agency judgments. As previously highlighted, the feeling of agency is not always sufficient for the judgment of agency; an evaluation of movement-outcome information is required (Haggard and Tsakiris, 2009).

4.5.2 The novelty P3: Anticipation and the judgment of agency

When there was no difference in fCRP amplitudes for sensory outcomes preceding agency and non-agency judgments (i.e. in the moderately-incongruent trial-type), the novelty P3 was the predictive indicator of the judgment of agency. The novelty P3 is commonly elicited by unanticipated sensory outcomes of voluntary movements (Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007), and engages attentional processes necessary for the evaluation of movement-outcome information (Chapter 2). As such, the P3 ERP family has been related to the evaluation of movement-outcome information in relation to previous experience (Chapter 2; Groen et al., 2007; Jongsma et al., 2006; Krigolson et al., 2009; Sailer et al., 2010).
It has been proposed that the judgment of agency is dependent on background beliefs about the causal factors of the sensory event in the current context (Synofzik et al., 2008a, b; Wegner, 2003). Thus, at the judgment of agency level, high-order cognitive authorship cues are included in the weighting process (Synofzik et al., 2008b). This would include movement heuristics associated with sensory outcomes (Chapter 2), as well as the general anticipatory cognitive state (Spengler et al., 2009; Wegner, 2003). Importantly, it has been proposed that weighting of these cognitive authorship cues occurs unconsciously, but when there is a discrepancy across multiple cues a conscious evaluation of movement-outcome information is initiated (Synofzik et al., 2008b). In fact, the novelty P3 has been linked to the involuntary capture of attention so that an unanticipated sensory outcome can enter conscious awareness (Friedman et al., 2001). Thus, the novelty P3 would index a large discrepancy across multiple authorship cues, which is necessary for conscious evaluation of movement-outcome information.

4.5.3 The fCRP and the novelty P3: Multiple factors in the judgment of agency

As highlighted by Wegner and Sparrow (2004), sensorimotor and cognitive authorship cues are convergent and complementary. In fact, the present results demonstrate that it was the distinction between novelty P3 and fCRP amplitudes that differentiated agency judgments from non-agency judgments. The weighting of fCRP and novelty P3 indicators for the judgment of agency differed across the trial-types. This is similar to the proposal that weighting of authorship cues differs among tasks and persons (Synofzik et al., 2008a, b). In general, when the fCRP indication of sensorimotor congruency and intentional movement-outcome coupling was stronger than the novelty P3 evaluation of authorship cue discrepancies, participants judged themselves as the agent of the sensory outcome.

However, there were a small proportion of non-agency judgments when movement-related perceptual cues indicated a high degree of congruency between visual feedback and internal predictions with an enhanced fCRP. This suggests that the explicit judgment of agency can be made independent of authorship cues. Furthermore, the different recognition or processing of authorship cues leads to agency and non-agency judgments within the same trial-type (which contain similar movement-related perceptual cues), highlighting the importance of the cognitive state at the time of the
sensory outcome (Wegner, 2003). Indeed, previous studies have demonstrated that modifying the content of conscious thought with movement related information can modulate the sense of agency (Moore et al., 2009; Wegner et al., 2004).

4.6 Conclusion

The present findings support multifactor and multilevel models of agency. The results highlight the monitoring role of the fCRP for the indication of sensorimotor congruency and intentional movement-outcome coupling. Conversely, the novelty P3 gauges discrepancies in anticipation across multiple authorship cues. Further investigations are required to elucidate how learning and the cognitive state may modify these ERP indicators and the sense of agency.
Chapter 5: General Discussion
Chapter 5
General Discussion

The consequences of voluntary movements are closely monitored and evaluated for future learning (Haggard, 2005), and it is the monitoring and anticipation of these consequences that allows for the sense of agency (Haggard and Tsakiris, 2009). This thesis examined outcome-related event-related potentials, namely the feedback correct-related positivity (fCRP) and the novelty P3, during various movement-related tasks, in order to investigate the cognitive processes that may govern outcome monitoring for future learning and the sense of agency. The concept of movement heuristics was proposed as a framework to theorise how movement-related and sensory information is monitored, evaluated, and integrated into an efficient set of rules to guide future behaviour, and mediate the sense of agency.

The discussion that follows begins by highlighting key ERP findings from each experimental chapter, and then extrapolates conclusions about the cognitive processes that underlie the monitoring of behavioural consequences. These findings and conclusions are synthesised with previous research to discuss the nature of the proposed movement heuristic and outcome-monitoring system, with suggestions for future work.

5.1 Movement heuristics are formed through an interaction between performance monitoring and evaluation

In Chapter 2, it was found that the amplitude of the feedback correct-related positivity (fCRP) was larger in response to sensory outcomes caused by the intentional movements of participants compared to sensory effects that were not caused by the movements of the participants. The amplitude of the novelty P3 demonstrated both stimulus-habituation and learning-related reductions. However, novelty P3 amplitude was enhanced when the unanticipated sensory outcome informed the learning of a movement heuristic compared to when the unanticipated sensory event indicated that a response was required. Enhancement of both fCRP and novelty P3 amplitudes was only observed during the acquisition of a movement heuristic. Based on these results (and what is known about the two ERPs of interest), it would appear that the formation of a movement heuristic depends on cognitive processes that 1) indicate a relationship
between the prior movement(s) and the sensory outcome, and 2) engage evaluative and integrative processes when an unanticipated sensory outcome is detected.

Previously, it was proposed that voluntary movements are acquired through an ideomotor learning process that associates consistently co-occurring movements and sensory outcomes (Elsner and Hommel, 2004; Elsner et al., 2002). Along these lines, Prinz (1997) suggested that an association between movements and their sensory outcomes is established through a common-coding process. Based on ERP findings, the fCRP may reflect the initial coding of movement-related information with sensory information. Evidence from previous studies demonstrating that the fCRP is enhanced to stimuli that are behaviourally relevant (Potts et al., 2006; Potts, 2004; Potts et al., 1996) supports this notion. However, the fCRP was also present in non-learning intentional movement tasks. Indeed, it has been proposed that the role of the fCRP in outcome monitoring is to indicate whether the task goal has been achieved (Hajcak et al., 2006; Holroyd et al., 2006; Holroyd et al., 2008). As a result, the improvement in behavioural performance and the acquisition of a movement heuristic appear to require additional cognitive processing.

Before a predictive link between intentional movements and sensory outcomes is established through learning mechanisms (cf. Haggard and Tsakiris, 2009), the sensory outcomes are initially unanticipated (Elsner and Hommel, 2001). To establish this link, learning would require the recognition and evaluation of unanticipated sensory outcomes. Indeed, the presentation of an unanticipated sensory outcome following a voluntary response elicits an orienting response and engages evaluative processes as indexed by the novelty P3 (Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007). Extending these studies, in Chapter 2 the presence of the novelty P3 indicated the need to recalibrate the established movement-outcome association (or movement-heuristic). This is supported by various studies demonstrating that the P3 is a predictive indicator of learning (Groen et al., 2007; Jongsma et al., 2006; Krigolson et al., 2009; Lindin et al., 2004; Sailer et al., 2010). Additionally, the main theoretical understanding of the P3, the context-updating theory, states that the P3 reflects the engagement of attentional processes to revise the current stimulus mental representation (Donchin, 1981; Donchin and Coles, 1988; Polich, 2007).
Importantly, the novelty P3 is also elicited by purely novel stimuli, and habituates with the repeated presentation of an initially novel stimulus (Friedman et al., 2001). In fact, in Chapter 2 a novelty P3 was elicited by unexpected sensory events that were unrelated to the previous motor movement. However, the amplitude of the novelty P3 was larger when the participants’ movements caused the unexpected sensory events. Additionally, the enhancement of the fCRP distinguished the novelty P3 that indicated the recalibration of a movement heuristic from the novelty P3 that simply indicated the occurrence of an unanticipated sensory event. By signalling that the sensory outcome was contingent on one of the preceding movements, processes underlying the fCRP would direct novelty P3 attentional processes to evaluate sensory information in light of the preceding movements. Thus, the formation of a movement heuristic is an interaction between performance monitoring, movement-goal coupling, and the evaluation of novel sensory information with regard to the preceding movement.

5.2 Enhanced basal ganglia signalling in medicated PD alters outcome monitoring

The ERP results from Chapter 3 demonstrated that individuals with Parkinson’s disease (PD) on dopamine medication had on overall enhanced novelty P3 compared to age- and sex-matched controls. fCRP amplitude in the stimulus-response task was also enhanced in persons with PD. Additionally, in PD patients no difference in fCRP amplitude was found between sensory outcomes caused by voluntary movements and sensory events not caused by the preceding movement.

At the start of this thesis, it was proposed that the basal ganglia, together with the anterior cingulate cortex (ACC) formed an outcome-monitoring system necessary for movement-outcome learning. The study reported in Chapter 3 was conducted to investigate the contribution of basal ganglia signalling to outcome monitoring, by testing people with mild to moderate PD. Previous studies have suggested that dopamine medication enhances basal ganglia signalling in individuals with PD (e.g. Cools et al., 2010; Frank et al., 2004; Moustafa et al., 2008; O'Reilly and Frank, 2006). Particularly signalling in intact corticostriatal loops (Cools et al., 2001; Gotham et al., 1988) such as the associative corticostriatal loop that is proposed to mediate movement-outcome learning (Balleine and O'Doherty, 2009). As a result, it was hypothesised that the cognitive processes underlying the monitoring and evaluation of movement-related
outcomes would be altered in medicated individuals with PD compared to normal controls.

In accordance with the proposal that dopamine medication in PD enhances the basal ganglia updating signal (Moustafa et al., 2008; O'Reilly and Frank, 2006), there was an enhancement in novelty P3 amplitude in medicated individuals with PD compared to age-matched controls. Of significance was the finding that this novelty P3 enhancement was observed only in conditions in which the novelty P3 was also elicited in controls (when the sensory event was associated with a degree of unexpectedness), and that enhancement of novelty P3 amplitude was not associated with a hindrance in learning or task performance. Thus, in medicated individuals with PD, the amplitude of the novelty P3 was enhanced, but the novelty P3 was not elicited erroneously. The movement heuristics to which the sensory outcomes were compared were not affected in PD. Rather, the results suggest that there was an enhanced updating signal elicited by the unanticipated sensory outcomes.

This enhanced updating signal in medicated individuals with PD engendered a coupling between their movements and the computer-controlled sensory event in the stimulus-response task, despite specific instructions to the patients that the sensory effect would not be caused by their movements. In control participants, and previously in undergraduates (Chapter 2), the fCRP was larger after sensory outcomes caused by the intentional movements of participants compared to sensory outcomes that were not caused by the movements of the participants. But this was not found in medicated PD patients. Consistent with this finding, Cools, Rogers, Baker, and Robbins (2010) suggested that the enhanced capture of attention by salient information in medicated PD patients was due to exaggerated bottom-up and/or attenuated top-down control. Additionally, it has been suggested that the top-down perceptions of the task or context requirements modulate the amount of attention allocated to bottom-up processes for outcome monitoring (Synofzik et al., 2008b). Thus, in medicated individuals with PD there may have been an enhanced bottom-up signal that overrode the descending top-down signal. This would result in sensory events not caused by the preceding movements to elicit an fCRP that was similar to the fCRP elicited by sensory outcomes that were caused by the preceding voluntary movements.
The increased coupling between movements and sensory events as described above is further consistent with other implications of research on people with PD. For example, this might be similar to the notion that pathological gambling in dopamine medicated PD participants is the result of a heightened sense of control (Moore et al., 2010b; Pessiglione et al., 2006; Voon et al., 2010). However, as highlighted by the literature on the sense of agency, in addition to sensorimotor authorship cues, there are cognitive cues that can influence the sense of agency (David et al., 2008; Synofzik et al., 2008b). Thus, while the fCRP response was similar across sensory events irrespective of whether those events were the cause of the participants’ movements, medicated individuals with PD could (at a higher cognitive level) know that their movements did not cause the sensory effect in the stimulus-response task. Following this trend, it is possible to speculate that higher doses of dopamine medication may increase the coupling between behaviours and outcomes, to a level that could induce this heightened sense of control.

The findings from Chapter 3 support the proposed outcome-monitoring system by demonstrating that altered basal ganglia signalling affects the monitoring and evaluation of outcomes; processes that are proposed to occur in the ACC (Rushworth et al., 2007b; Walton et al., 2004).

5.3 The judgment of agency arises from the weighting of movement-outcome coupling and outcome anticipation

Overall, in the judgment of agency task employed in Chapter 4, agency judgments were preceded by sensory outcomes that had a larger fCRP compared to sensory outcomes that preceded non-agency judgments. When fCRP amplitudes were not significantly different, a larger novelty P3 indicated that the sensory outcome was unanticipated, which in turn resulted in non-agency judgments. In fact, in conditions where sensorimotor cues did not imply a causal connection between intentional movement and the sensory outcome, the difference between novelty P3 and fCRP amplitudes was predictive of the judgment of agency.

Our sense of agency originates from learning mechanisms that associate voluntary movements and sensory outcomes that often occur together (Hommel and Elsner, 2009). Learning establishes the predictive link between intentional movements
and sensory outcomes that give rise to the sense of agency (Haggard and Tsakiris, 2009; Spengler et al., 2009). As demonstrated in Chapter 2, movement-outcome learning is dependent on the interaction between the fCRP and the novelty P3, with the fCRP indicating sensory outcomes that were the result of one’s own behaviour.

Following this trend, in Chapter 4 the fCRP was the main predictor of agency judgments. Li et al. (Li et al., 2011) has demonstrated that the sense of control, similar to the feeling of agency, can modulate outcome monitoring akin to the fCRP. In line with Synofzik, Vosgerau, and Newen (2008a), the fCRP in the present study signalled the degree of coupling between intentional movements and the sensory outcome. There was no significant difference in fCRP amplitude for sensory outcomes that led to agency judgments. Thus, while the highest proportion of agency judgment occurred when sensorimotor cues indicated a congruency between the predicted and actual sensory outcome, agency judgments across the different conditions were made based on the degree of coupling between movements and the sensory outcome. This movement-outcome coupling, while presumably influenced by the output of an internal comparator (Berti et al., 2005; Blakemore et al., 2002), was not solely dependent on congruent output (Synofzik et al., 2008a, b).

In addition to fCRP amplitude, the amplitude of the novelty P3 was also an integral factor in the judgment of agency. The P3 ERP family is theorised to predominately mediate high-order evaluation of sensory information deemed unexpected, based on previous experience and context (Donchin and Coles, 1988; Mars et al., 2008; Waszak and Herwig, 2007). This would include movement heuristics associated with sensory outcomes, as well as the general anticipatory cognitive state (Spengler et al., 2009; Wegner, 2003). Along these lines, it has been proposed that weighting of these cognitive authorship cues for the judgment of agency occurs unconsciously; however, when there is a discrepancy across multiple cues a conscious evaluation of movement-outcome information is initiated (Synofzik et al., 2008b). Thus, the novelty P3 would index a large discrepancy across multiple authorship cues, engaging conscious evaluation of movement-outcome information. This would allow for either the updating of the movement heuristic in learning contexts (Chapters 2 and 3) or the determination that the unanticipated sensory outcome was not caused by one’s own movements.
By measuring outcome-related ERPs during a judgment of agency task, this study assists with understanding how anticipation and monitoring of the sensory outcomes of voluntary movements give rise to the sense of agency. The findings from this study suggest that the monitoring of sensory outcomes to establish the degree of coupling between voluntary movements and the task goal, and this is reflected in the amplitude of the fCRP component. While this initial feeling of agency (Synofzik et al., 2008a) normally leads to judgments of agency, the subsequent indication the novelty P3 that the sensory outcome was unanticipated (based on previous experience) can supersede the feeling of agency, resulting in judgment of non-agency. Thus, the results of this study provide a potential neural basis for multifactor and multilevel accounts of the sense of agency (e.g. Synofzik et al., 2008a, b; Wegner and Sparrow, 2004).

5.4 Extensions of findings

5.4.1 Forming a movement heuristic

Humans perform a variety of movements to obtain and respond to a variety of sensory consequences. To maintain this adaptable behaviour the brain is actively monitoring sensory and cognitive information to glean essential associations used to efficiently guide behaviour (Bar, 2007). Along these lines, the brain has a propensity to economise cognitive resources, while at the same time optimising behaviour (Franz and McCormick, 2010). Following this trend, the concept of movement heuristics was proposed to capture the required flexibility of adaptive learning.

To differentiate learning a movement heuristic from previous ideomotor paradigms that established a simple one-to-one association between movement and outcome (e.g. Elsner and Hommel, 2001, 2004; Waszak and Herwig, 2007), a novel movement-learning task was developed in this thesis. The employed movement-learning task (Chapters 2 and 3) required a ‘flexible learning’ approach. A specific movement did not cause the sensory outcome like in previous ideomotor paradigms in the literature (e.g. Elsner and Hommel, 2004; Elsner et al., 2002). Rather, in this task, the occurrence of the sensory outcome depended on the end location of the movement, with the starting location of the movement varying from trial to trial. As a result, learning did not involve associating the specific mechanics of a movement to a specific outcome, but instead gleaning the principal aspects of the movement(s) that elicited the
sensory outcome. Thus, while multiple movements could elicit the desired sensory outcome, improved performance was dependent on establishing a movement heuristic based on the principal aspects common across all movements. In this manner, the movement-learning task study considerably differs from and extends ideomotor learning to a more general context of learning.

5.4.2 The importance of intention and context

As demonstrated in Chapter 2, the formation of a movement heuristic was dependent on an initial movement-outcome coupling, and the evaluation of novel sensory information in light of this movement-outcome coupling. Indeed, fCRP amplitude was enhanced only by sensory outcomes produced by intentional movements (Chapter 2), thus highlighting the importance of intention. Supporting the importance of intention, previous studies have demonstrated that the ideomotor learning process is unique to intentional-based movements (Herwig et al., 2007; Herwig and Waszak, 2009). Along these lines, unanticipated sensory outcomes caused by intentional movements elicited a novelty P3 that was larger than unanticipated sensory effects controlled by a computer (Chapter 2).

The coupling between intentional movements and sensory outcomes likely stems from (the previously-described finding) intentional performance of a movement altering the perception of time between the movement and a sensory outcome, so that they appear closer in time (Haggard et al., 2002). Interestingly, the lack of learning-related changes in fCRP amplitude (Chapters 2 and 3) suggests that this coupling is not dependent on a learned association between movements and outcomes. As demonstrated in the judgment of agency task in Chapter 4, a discrepancy in sensorimotor information did not always prevent movement-outcome coupling. Thus, it appears that intention creates a bias to associate movements with outcomes.

The context in which a movement is performed shapes how the outcomes are monitored. Instructions to the participants that the sensory effect was not caused by their movements reduced outcome monitoring and evaluation as shown by a reduced fCRP and novelty P3 amplitudes, despite the fact that the sensory effect was behaviourally relevant and temporally unexpected (Chapter 2). Additionally, the interpretation of the novelty P3 is modulated by task context; during learning the
presence of the novelty P3 indicated the need to recalibrate the movement heuristic (Chapter 2). In contrast, during the judgment of agency task the presence of the novelty P3 indicated that the sensory outcome was not the result of one’s own movements (Chapter 4). Together these findings would support the proposal that top-down perceptions of the task or context requirements modulate the amount of attention allocated to bottom-up processes for outcome monitoring (Synofzik et al., 2008b). Conversely, enhancing bottom-up signalling (via dopamine medication) may override this top-down modulation resulting in a heightened sense of control (Chapter 3). Therefore, it is speculated that while intention and context appear to greatly influence outcome monitoring and evaluation, proper bottom-up processing is still vital for the formation of movement heuristics.

5.4.3 Outcome-monitoring system

The basis of this investigation was the proposal that the basal ganglia and the ACC interact to provide a learning and monitoring system to shape and determine voluntary behaviours. The basal ganglia were proposed to register the occurrence of behaviourally relevant outcomes (Zink et al., 2003), and converge on the causal aspects of movement and context that elicited the sensory outcome (Redgrave and Gurney, 2006; Redgrave et al., 2008). Furthermore, it was proposed that this information was relayed to the ACC where outcome-related ERPs are generated (e.g. Zhou et al., 2010). Importantly, the ACC has been proposed to generate intentional movements (Paus, 2001), and also monitor, evaluate, and integrate the outcomes of intentional movements to guide future behaviour (e.g. Holroyd and Coles, 2008; Rushworth et al., 2007a; Walton et al., 2004). Below, the ERP findings from this thesis are synthesised with previous findings in the literature to make inferences about the proposed outcome-monitor system.

5.4.4 The fCRP reflects the intrinsic basal ganglia process of agency identification

It has been proposed that the phasic dopamine signal carried by the midbrain dopamine system to the ACC is responsible for the occurrence of the fCRP (Holroyd and Coles, 2002; Holroyd et al., 2008). Supporting this notion, previous studies have demonstrated that there is a link between dopamine activity in the basal ganglia and the fCRP (de Bruijn et al., 2005; Potts et al., 2006). This phasic signal is elicited by
unexpected stimuli (Freeman et al., 1985; Horvitz et al., 1997; Schultz, 1998), and through modulation of efficacy on corticostriatal synapses (Reynolds et al., 2001), the phasic dopamine signal is proposed to mediate reinforcement learning.

In Chapter 3, it was found that individuals with PD on dopamine medication had an enhanced fCRP only in the stimulus-response task, unlike normal controls. Conversely, an enhancement of the novelty P3 in dopamine medicated PD patients was observed across all tasks with unexpected sensory effects (Chapter 3). Additionally, the fCRP overall did not demonstrate learning related changes and was elicited by expected sensory outcomes in non-learning tasks (Chapters 2 and 3). Collectively, these results would suggest that the fCRP might not directly reflect the neural processes related to the phasic dopamine signal. As an alternative, the fCRP might reflect the output of an intrinsic basal ganglia process of agency identification.

Sensory, motor, and contextual inputs from cortical and subcortical structures converge in the basal ganglia (Alexander et al., 1986; McHaffie et al., 2005; Mink, 1996). This convergent macro-architecture allows the basal ganglia to monitor a large and diverse set of information. Through an intrinsic process of comparing the ‘salience’ of these different input signals (Gurney et al., 2001; Redgrave et al., 2008), the basal ganglia select important or behaviourally relevant information that should be monitored and evaluated by the ACC and other cortical structures. The regulation of input saliencies is likely mediated by dopaminergic modulation of the efficacy of corticostriatal synapses (Reynolds et al., 2001). Additionally, top-down perceptions of the task or context requirements (e.g. intention) could also modulate input saliencies. This may occur through cortical adjustment of dopamine neuron activity. Along these lines, the ACC has projections to dopamine neurons (Garaino and Groves, 1988). Thus, when intentional movements are generated by the ACC (Paus, 2001), the ACC could additionally enhance input saliencies in the basal ganglia via activity on the dopamine neurons. Conversely, when outcomes are known to be unrelated to the performed movement, the same mechanism could reduce input saliencies.

This top-down modulation of input saliencies via adjustment of dopamine neuron activity is supported by the fCRP findings. Specifically, individuals with PD on dopamine medication had an enhanced fCRP only in the stimulus-response task. Since dopamine medication does not restore the function of degenerated dopamine neurons,
but instead increases the level of dopamine within the basal ganglia, the ACC would not be able to adjust input saliencies in the basal ganglia. As a result, there would be no difference in outcome monitoring across goal-directed and stimulus-response tasks (Chapter 3). In conclusion, by allowing intention to modulate basal ganglia signalling, this mechanism would support an intrinsic process of agency identification reflected by the fCRP.

5.4.5 The novelty P3 reflects ACC evaluation of outcomes driven by the phasic dopamine signal

The novelty P3 demonstrated learning-related reductions with improved task performance (Chapter 2), and was additionally enhanced in dopamine-medicated PD patients (Chapter 3). In general, the novelty P3 is elicited by novel/unanticipated stimuli (Friedman et al., 2001), or stimuli that differ from the current mental representation (Waszak and Herwig, 2007). Likewise, unexpected sensory events induce a phasic signalling in dopamine neurons (Horvitz et al., 1997 Ljungberg et al., 1992a). This suggests a potential link between the ACC generated P3 (specifically the P3a/novelty P3; Polich, 2007; Zhou et al., 2010) and the phasic dopamine signal.

The novelty P3 appears to be modulated by the formation of a movement heuristic. As a result, a mechanism by which the ACC could modify the afferent sensory processing of dopamine neurons would be required. Previous studies suggest that the superior colliculus is the source of afferent sensory input to dopamine neurons (Coizet et al., 2003; Comoli et al., 2003; Dommett et al., 2005). The superior colliculus is commonly activated by novel or behaviourally relevant stimuli (Ikeda and Hikosaka, 2003), and provides the quick indication of a change in the environment eliciting an orienting response (Grantyn, 1988). Notably, the superior colliculus is among the ‘attentional’ brain regions that receive dense norepinephrine projections (Aston-Jones and Cohen, 2005; Foote and Morrison, 1987). Furthermore, the ACC along with the orbital frontal cortex (brain region associated with reward processing) has strong convergent inputs to the locus coeruleus, the brain region responsible for the release of norepinephrine (Aston-Jones and Cohen, 2005). Along these lines, ACC evaluation of sensory and movement-related information could create a movement heuristic that would be used via modulation of locus coeruleus activity to set the sensitivity of the superior colliculus. As a result, sensory outcomes exceeding the set threshold would
activate the superior colliculus, leading to phasic activity of the dopamine neurons. Additionally, the ACC can further modulate the salience of a sensory outcome through modulation of dopamine release (Gariano and Groves, 1988). Collectively, these hypothesised ACC modulatory inputs into the norepinephrine and dopamine systems would indicate whether a sensory outcome was unanticipated by the current movement heuristic (Figure 5.1).

![Figure 5.1](image_url) Proposed outcome-monitoring and evaluation system. Modulation of the locus coeruleus (LC) norepinephrine system (pink arrows) by the anterior cingulate cortex (ACC; purple lines) would change the sensitivity of the superior colliculus (SC), which in turn indirectly modulates substantia nigra pars compacta (SNpc) dopamine neurons. Additionally, ACC activity can directly modulate the activity of dopamine neurons. Dopamine activity (orange arrows) would highlight important motor (green arrows), context (blue arrows), and sensory (red arrows) information that are relayed to the ACC via the thalamus. This information would be subsequently used to inform ACC directed movement-selection and modulation of the norepinephrine and dopamine systems. Cortical inputs would also modify ACC activity.

Furthermore, it is possible to speculate that the phasic dopamine signal would initiate the attentional processes underlying the novelty P3. As such, novelty P3 activity would index ACC evaluation of movement and contextual information related to the unanticipated sensory event. However, previous studies have associated the P3 ERP family with a variety of neuromodulators including dopamine (Polich and Criado, 2006), norepinephrine (Nieuwenhuis et al., 2005), and acetylcholine (Dierks et al.,
1994). Yet, although it is unlikely that the novelty P3 is directly elicited by the phasic dopamine signal, the novelty P3 may reflect a cascade of neural events associated with the phasic dopamine signal. Thus, learning-related reductions (Chapter 2), and an overall enhancement in dopamine-medicated PD patients (Chapter 3), suggest that the novelty P3 elicited during the movement-learning task reflects ACC evaluation of outcome driven by the phasic dopamine signal.

5.5 Future work and recommendations

While this research has begun outlining outcome-related cognitive processes that mediate the formation of movement heuristics and the sense of agency, many questions remain. The first priority is to understand how the content of conscious thought modifies outcome monitoring and anticipation. Perhaps the most interesting result from this thesis was how intention and context shape the monitoring and evaluation of outcomes. Previous studies have suggested that the mode of movement, task perceptions and context adjust the amount of attention given to bottom-up processes (Haggard et al., 2002; Haggard and Tsakiris, 2009; Synofzik et al., 2008a, b; Wegner et al., 2004). While the present findings support this notion, the question remains whether there are measureable changes in brain activity that would bias the monitoring and evaluation towards movement-outcome coupling, and the sense of agency. Moore, Wegner, and Haggard (2009) induced a sense of agency through the use of a supraliminal prime that corresponded with the outcome of the subsequent voluntary or involuntary movement. It was proposed that the external cue modified the content of conscious thought prior to movement, thus potentially inducing the experience of intentionally initiating movements. A similar design could be used to investigate brain activity to supraliminal primes, and the subsequent sense of agency.

The goal of the movement-learning task employed in this thesis was to investigate the formation of movement heuristics. The task involved participants learning that the principal aspect common to all movements eliciting the sensory outcome was the end location. While the movement-learing task was more flexible than the typical one-to-one movement-outcome associations commonly employed in ideomotor learning paradigms (e.g. Elsner and Hommel, 2001, 2004; Herwig and Waszak, 2009) additional studies are required to fully capture the potential extent of the flexibility and plasticity of movement heuristics. This may include studies that
distinguish the what, where, and when of movement contingencies, as well as measuring brain activity during real world tasks such as opening a variety of doors, or turning on various types of light switches.

Of particular interest is the learning context. In Chapters 2 and 3, participants were informed that the movement-learning task had a learning aspect, and that their movements would cause the sensory outcome. Yet, in everyday life, learning and causation are not typically predefined. As a result, conditions and cues that predispose a sense of agency over sensory events become prerequisites for learning and acquiring new movement heuristics. In these uncertain conditions, the phasic dopamine signal may be vital for the initial linking of motor activity and sensory information within the basal ganglia (Redgrave and Gurney, 2006; Redgrave et al., 2008).

By examining the fCRP and novelty P3 in dopamine-medicated individuals with PD, this thesis highlighted the importance of basal ganglia signalling for the monitoring and evaluation of sensory events. While previous studies indicate that dopamine plays essential roles in both the fCRP and novelty P3 (e.g. Holroyd and Coles, 2002; Polich and Criado, 2006; Santesso et al., 2009), the inherent spatial limitations of EEG recording and variation in dopamine medication dosage in PD patients restrict any direct accounts of basal ganglia and dopamine contribution to outcome-related ERPs. Additionally, it remains to be determined whether the effects of dopamine medication observed in PD patients are the result of enhanced dopamine signalling along the lines of the dopamine overdose hypothesis, or due to an inability to control dopamine release because of dopamine neuron degeneration. Studies comparing neuropharmacological manipulations of dopamine activity in normal controls to individuals with PD could help elucidate this dopamine medication effect in PD.

The fERN and the fCRP appear to be opposing responses of similar outcome monitoring processes (Hajcak et al., 2006; Holroyd et al., 2008). As such, there is priority to investigate the role of negative feedback in learning, and how negative feedback is processed in medicated PD. Recently, Santesso et al. (2009) demonstrated that using a low dose of a dopamine agonist hinders reinforcement learning and enhances the fERN. Additionally, based on a decreased sensitivity to negative outcomes in dopamine medicated PD patients (Frank et al., 2004), it has been proposed that their behaviour is biased toward positive outcomes, which in turn may be
responsible for occurrence of pathological gambling in PD (Pessiglione et al., 2006; Voon et al., 2010). The results in this thesis suggest a bias towards movement-outcome coupling in medicated PD. However a further investigation is needed to determine whether this coupling is differentially modulated by the valence of the outcome, because there may be a decreased sense of agency over negative outcomes in dopamine medicated PD.

5.6 Conclusions

This thesis provides a foundation for the ERP-based study of cognitive processes that may govern outcome monitoring for future learning and the sense of agency. By combining systematic manipulations of tasks along with investigations in a population of neurologically impaired individuals the present thesis has used a convergent approach to elucidate functional significance of the fCRP and the novelty P3 in outcome monitoring and evaluation. Collectively, the findings highlight the role of the fCRP in coupling movements with sensory outcomes, and the role of the novelty P3 in evaluating novel sensory information with regard to the preceding movement. Furthermore, the results suggest that these processes of monitoring and evaluation are generated by a cascade of neural events governed by interactions between the ACC and basal ganglia structures. Yet, further investigations are required to elucidate how learning and the cognitive state may modify these ERP indicators and the sense of agency. Finally, the results support the concept of movement heuristics to guide future behaviour, and mediate the sense of agency.
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